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UNDERSTORY RESPONSE FOLLOWING TWO
SOUTHWESTERN FIRES

Understory Response Following Two Southwestern Fires

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Submitted to:

Dr. Carolyn Hull Sieg
USDA Forest Service, Rocky Mountain Research Station

Submitted by:

Peter Z. Fulé, Associate Professor and Associate Director
Rita S. Dodge, Conservation Botanist/Director, Red Butte Garden and Arboretum, UT

Ecological Restoration Institute and School of Forestry
Northern Arizona University
P.O. Box 15018, Flagstaff, AZ 86011
(928) 523-1463, fax (928) 523-0296

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Contents

Executive Summary.....	2
Project Accomplishments.....	3
Appendix 1: Understory response following two southwestern wildfires	4
Appendix 2: Dalmation Toadflax Response to Wildfire and Native Species Revegetation in Ponderosa Pine Forest	25



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240 W Prospect Rd
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Executive Summary

Recent fires in northern Arizona offer a unique opportunity to investigate understory response in large forested landscapes where the context of pre-burn forest structure, fire regime, and fire hazard is well understood. The Leroux fire, on the Coconino National Forest, and the Tower fire, in Grand Canyon National Park, burned in 2001. Both fires covered several thousand acres in pre-existing study areas where the understory vegetation, fire disturbance regime and forest structure had already been measured. Fire severity varied in both fires from unburned or minimally burned areas to areas that burned with stand-replacing fire. We examined the understory response to wildfire and the relationship between wildfire and exotic species invasion with three original goals:

1. Quantify the understory vegetation response in pre-existing plots following the burns;
2. Quantify the response of native and exotic species to wildfire relative to variations in burn severity;
3. Using data on existing exotic invasive plant species, develop field or greenhouse experiments to test specific hypotheses about the role of fire severity in assisting the spread of these species.

Because of the small size and low number of plots ($N = 6$) in the Tower Fire, the strength of inference was limited. However, few exotic species were encountered after the fire and the plant community changed minimally. These findings were consistent with the relatively unperturbed site, affording minimal opportunity for exotic plant propagules to enter, and the low severity of the fire. Details are presented in Appendix 1.

The Leroux fire, with a much larger data set, offered a more substantial basis for study. Details of the following two research projects are presented in an M.S. thesis, attached in Appendix 2. Within the context of ecological restoration, the goal of this study was to assess disturbance, exotic species, and native plant revegetation in two complementary ways. The increased size of severe fires in recent years in the southwestern U.S. has created large patches of higher severity burns that are available for colonization and spread of invasive exotic species and may require revegetation. We measured (1) the response of Dalmatian toadflax growth and reproduction to varying burn severity; and (2) the impact of toadflax on the native understory community, for three years after a wildfire in the ponderosa pine forest of northern Arizona. Toadflax density, cover, and flower stalks increased in the second year, then declined slightly in the third year in each burn severity class, although all variables remained higher in the third year than in the first. Change in toadflax variables from 2002 to 2003 differed ($p < 0.001$) among fire severity classes, with the greatest increase on high severity plots. In contrast, change in toadflax variables from 2003 to 2004 only differed among toadflax density classes ($p < 0.001$). Although toadflax declined in plots by the third year, we found evidence of spread into previously uncolonized areas surrounding plots. Native species richness differed among burn severity classes, and was not correlated to toadflax density or cover. We recommend focusing control efforts on high and moderate burn severity areas. Toadflax variables increased the most in the low density class, therefore

control efforts should be focused at the periphery of large patches or on new satellite population where density is low.

Revegetation is one of the most common and economically efficient practices to restore disturbed areas by increasing native species richness and abundance, and reducing exotic species invasion. The second study evaluated the germination and growth performance of 28 native southwestern species and one exotic grass species to indicate their success for accomplishing revegetation goals. We conducted three seed performance trials in a germination chamber, a greenhouse, and in the field and developed an integrated relative species performance rating. Cool season grasses and forbs had higher average germination in all three trials and higher cover and biomass production during the first field season than warm season species. Grass germination was slightly higher than forbs in the field, but provided twice as much cover by the second field season. Species with the highest overall field performance ratings were squirreltail (*Elymus elymoides*), blue gramma (*Bouteloua gracilis*), purple locoweed (*Oxytropis lambertii*), and ragleaf bahia (*Bahia dissecta*). The exotic annual ryegrass (*Lolium multiflorum* var. *gulf*) did not perform better than native grasses or forbs in the field, therefore, we do not recommend not using this species over native grasses for revegetation in the southwestern U.S. We recommend a combination of cool and warm season grasses and forbs to provide plant cover all year and accomplish revegetation goals.

Project Accomplishments

The following accomplishments have been achieved to date in this project:

M.S. Thesis:

Rita S. Dodge. 2004. Dalmation toadflax (*Linaria damatica*) response to wildfire and native species regeneration in ponderosa pine forest. School of Forestry, Northern Arizona University.

Publication in review:

Dodge, R.S., P.Z. Fulé, and C.H. Sieg. Dalmatian toadflax (*Linaria dalmatica*) response to wildfire in a southwestern forest. *Ecoscience*.

Presentation:

Dodge, R.S. Dalmatian toadflax (*Linaria dalmatica*) response to the Leroux wildfire. San Francisco Peaks Weed Management Group meeting, September 2004.

Appendix 1: Understory response following two southwestern wildfires

Understory Response Following Two Southwestern Wildfires

Final Report

Rita Dodge and Peter Z. Fulé

Introduction

Climate and fire are the two primary environmental processes which drive the structure, composition, and function of the southwestern ponderosa pine forest. These natural processes interact with the vegetation communities by influencing individual species survival and establishment, community composition, individual and community spatial distribution, and overstory vertical and age structure. An important difference between these two processes is that climatic processes can independently affect the vegetation community without the presence of fire. However, since climatic processes are continuous, it is not possible for fire to affect the vegetation community independent of climate. Therefore any fire effects research must also consider any effects due to climate. Plant community changes are more rapidly evident in the understory due to a higher degree of biodiversity and shorter life-cycles than overstory species. To investigate the effects of wildfire on the vegetation community in the southwest, this study looks at changes in the pre and post-fire understory community after two wildfires which occurred during a period of severe drought.

The understory vegetation of the southwestern ponderosa pine forests is composed of diverse graminoids, forbs, and shrubs. These species contribute almost all of the plant biodiversity in the ecosystem, since there are typically fewer than 4 overstory species present (Korb and Springer 2003, Naumberg and DeWald 1999). The understory community plays critical roles in the ecosystem by providing wildlife forage and habitat, limiting ponderosa pine seedling establishment through competition, recycling nutrients, retaining soil, promoting surface fires, maintaining biodiversity, and reducing exotic invasion (Korb and Springer 2003, Moore et al. 1999). Early seral understory species are the first to colonize disturbed areas; and this early colonization by native species can prevent or reduce the establishment of exotic, invasive species (Griffis et al. 2001, Tilman 1997). Fire also plays key roles in southwestern ponderosa pine forests by regulating pine seedling establishment, nutrient cycling, understory composition, reducing fuel accumulation, maintaining open grassy spaces, and creating wildlife habitat (Fulé et al. 1997, Covington and Moore 1994). The response of understory vegetation to fire varies greatly depending fire severity, size, pre-fire vegetation, soil seed banks, soil type, climatic variation, and individual species responses (Korb and Springer 2003, Crawford et al. 2001). Weaver (1951) reported that prescribed burning increases perennial grass productivity in ponderosa pine forests. While benefiting native species, fire has also been demonstrated to disproportionately benefit exotic species by increasing foliar cover and richness within Northern Arizona ponderosa forests (Griffis et al. 2001, Crawford et al. 2001). Griffis et al. (2001) also found that native species richness, composition, and cover varied significantly at different fire severity levels.

The fire regime and behavior has changed over the past century from frequent, low-severity fires, to large, high-severity crown-fires that the western United States is currently experiencing. Prior to European settlement, southwestern ponderosa pine forests were characterized by clumps of ponderosa pines in relatively open forests or savannahs (Cooper 1960). These forests were maintained by frequent low-intensity ground fires at approximately 2-12 year (Cooper 1960, Weaver 1951) or 2-20 year intervals (Swetnam and Baisan 1996). European settlement of the Southwest brought with it the widespread practices of fire suppression, domestic livestock grazing, road construction, and logging which have created current forest conditions characterized by high fuels accumulation, dense "dog hair thicket" stands, low understory diversity, slow nutrient cycling, and high severity crown fires (Covington et al. 1997, Covington and Moore 1994). These land management practices have altered the fire-regime, fire behavior, forest structure and function, and understory abundance and composition (Covington et al. 1997, Moore et al. 2006). The native vegetation is neither adapted to the overcrowded forest conditions nor to the current 'historically unnatural' fire regime. Since these large high-severity fires are a relatively recent occurrence, the effects of recent fires on understory species are largely unknown.

In order to understand how the understory is affected by these fires today, we must also have knowledge about the understory community prior to settlement, or reference conditions. Effects of post-

settlement land management practices on the ponderosa pine overstory have been well documented through dendrochronology and fire scar dating; however, these methods can only relate historical patterns of overstory species. The same methods can not be applied to understory species due to their lack of woody tissue and rapid decay. Our knowledge about understory composition and fire response prior to European settlement is limited to qualitative historic cultural accounts, photographs, and paleoecology (Weaver 1951, Korb and Springer 2003, Sieg et al. 2003). There is also lack of quantitative knowledge about current patterns of understory recovery following recent intense, large-scale fires in southwestern ponderosa pine forests (Gildar et al. 2004, Crawford et al. 2001, Huisinga et al. 2005). Poor understanding of reference conditions and variable responses make it difficult for present land managers to develop post-fire restoration plans.

One way to reconstruct historical understory community composition is by studying relatively undisturbed "relict" sites. Relict sites act as modern reference condition sites and have remained relatively undisturbed but have been subject to present-day climatic conditions. This information can then be compared to the understory response of post-settlement disturbed sites, and applied in current ecosystem restoration decisions (Gildar et al. 2004). Due to intensive grazing and logging, areas that can serve as reference sites are rare and most suitable reference sites are found within protected areas, such as national parks (Fulé et al. 2002). The Grand Canyon's North Rim is one such protected area where grazing has been excluded for decades and fire has occurred regularly (Korb and Springer 2003), and serves as one of our study sites. The Tower fire at Grand Canyon National Park, Arizona, and Leroux fire near Flagstaff, Arizona provided an opportunity to compare understory responses of two wildfires occurring in the same year and with different management histories.

Since wildfire occurrence is unpredictable, most fire studies take place after the fact, and as a result, it is often difficult to draw clear conclusions about fire effects on the ecosystem. The inferential difficulties associated with wildfire can be minimized by incorporating pre-burn information, measuring unburned sites, and studying multiple fire events. A unique feature of this project is that we have detailed pre-fire data on forest overstory, understory, and fuels at both study sites from plots previously established for an ongoing fire-modeling project. The opportunity to use pre-burn vegetation data is rare, and can provide valuable information for land managers in predicting the effects of wildfire, or prescribed fire on current understory communities.

Methods

Study Area

The September 2001 Tower fire burned within Grand Canyon National Park (GCNP) on the North Rim near Galahad point (Figure 1). The lightning-caused fire burned 4,063 acres of ponderosa pine and mixed conifer forest. Fire severity was low to moderate with no tree mortality. The June 2001 Leroux fire occurred on the south side of Agassiz Peak within the San Francisco Peaks-Kachina Peaks Wilderness Area of the Coconino National Forest. The human-caused fire burned 1,200 acres of ponderosa pine, mixed conifer, and aspen forest between the elevations of 2,493 m (8,180 ft) to 3,145 m (10,320 ft), with Freidlein Prairie Road as the southernmost border (Figure 2). Fire severity ranged from low in grassy open patches to high in densely treed patches, creating a mosaic pattern of burn severity across the landscape (Cocke et al. 2005a, b). High tree mortality rates occurred within the moderate and high severity patches.

Fire exclusion policies have been in place at both sites since circa 1880 and both are currently managed as wilderness areas. Livestock grazing was allowed at Galahad Point from 1870 – 1938, though it was never logged (Fulé et al. 2003). The Kachina Peaks Wilderness Area was established in August 1988 by the Arizona Wilderness Act. Grazing has occurred within the Kachina Peaks Wilderness historically and is currently allowed, though in recent years the permit owner has maintained it as a non-use permit (Katherine Farr, US Forest Service, personal communication 2004). Timber harvesting was allowed prior to designation as a wilderness; however steep slopes meant that most harvesting occurred at elevations below the current wilderness boundary (Katherine Farr, US Forest Service, personal communication 2004). Due to difficult access, Galahad Point sees limited human influence and recreational use. However, the Kachina Peaks Wilderness Area is easily accessible to both day and overnight users through an extensive trail system, established campsites, and roads.

The San Francisco Peaks are also sacred to several Native American tribes who have used the area for religious and medicinal purposes for decades.

Soils at Galahad point are Typic Paleustalfs (Fulé et al. 2003) and the site has an average slope of 16.3%. Average annual precipitation is 63.7 cm, with an average snowfall of 349.5cm recorded at the North Rim Ranger District station from 1948-2003 (Western Regional climate Center 2004, www.wrcc.dri.edu). Average annual temperatures range between 13.56°C maximum in July and -0.83°C minimum in January. There was a significant difference in precipitation between the three years of data collection; annual precipitation at the Grand Canyon NP 2 station was 34.67 cm in 2000, 47.45 cm in 2001, and 22.68 cm in 2002 (Western Regional climate Center 2004, www.wrcc.dri.edu). Soils in the Leroux fire area of the Kachina Peaks Wilderness are basalt derived and the site has an average slope of 18.25%. Average annual precipitation is 57.05 cm, with an average snowfall of 214.38 cm recorded at the Fort Valley station from 1909-2003 (Western Regional climate Center 2004, www.wrcc.dri.edu). The Fort Valley records were incomplete, but the Flagstaff WSO station recorded annual precipitation at 39.06 cm in 2000, 44.58 cm in 2001, and 32.72 cm in 2002 (Western Regional climate Center 2004, www.wrcc.dri.edu). Differences in yearly precipitation during these years at the Leroux fire site were not statistically significant.

Plot Measurements

Sampling plots were established for a landscape fire modeling project at both Gallahad Point and the San Francisco Peaks; detailed descriptions of plot selection methods can be reviewed in Covke et al. (2005a). In brief, sampling plot centers were located from a 300-m systematic grid placed over each sampling site. The grid spacing was designed to measure fire and forest structure at a large scale, consistent with the expectation of large fires under a mixed-severity fire regime. Sampling plots were 0.1 ha (20 x 50 m) in size, oriented with the 50-m sides uphill-downhill to maximize sampling of variability along the elevational gradient and enable correction of the plot area for slope. Plots were established to measure current conditions of overstory structure, understory composition, fuel, and dendroecological data (Fulé et al. 2003, Cocke et al. 2005a, b). However, this study is restricted to the understory vegetation response following these two wildfires while taking advantage of rare pre-fire data collected for the landscape fire modeling project. Sixteen of these pre-existing plots were burned in the Leroux fire and six plots in the Tower fire. Leroux Fire plots were measured for two years, 2000 (pre-fire) and 2001 (post-fire), and Tower fire plots were measured for three years, 2000 (Pre-fire 1), 2001 (pre-fire 2), and 2002 (post-fire).

Understory vegetation was sampled along the two 50-m boundaries of each plot using point line-intercept methods. Species identification, height, and substrate type (litter, wood, soil, rock) were recorded every 30 cm along each transect, totaling 332 points per plot. Species presence was recorded within a 50 X 10m belt overlaid on each transect. Canopy cover was measured every 3 m along the 50-m transect by vertical projection (Ganey and Block 1994). Identical techniques were used for pre- and post-fire measurements at both sites.

Statistical Analysis

Total plant frequency, exotic plant frequency, frequencies of individual species and groups of species, and species diversity (Shannon's H) were calculated from point-line intercept data. We divided all species at the Leroux site into one of the following functional groups: tree, shrub, legume, perennial forb, annual forb, C₃ grass, C₄ grass, or parasite (Tilman et al. 1997). We used belt transect data to calculate species richness.

Some understory plants were difficult to identify in the field, so it was necessary to group certain taxa by genus for analysis (eg. *Bromus anomolus* and *Bromus ciliatus* were called *Bromus* spp.). For this reason, species richness and species diversity measures are underestimates. Each species' origin was classified as native or exotic (Tables 1 and 2). There is considerable debate in the literature and among botanists about the accuracy of identification of *Chenopodium album*, as well as its origin classification. Due to this uncertainty we did not classify *C. album* as an exotic species for analysis.

Multivariate repeated measures analyses were carried out to test for a significant wildfire effect. SPSS software version 11.5 and JMP version 5.0 were used for parametric and nonparametric univariate analyses. All variables used in parametric tests were checked for normality and equal variance by confirming that the Shapiro-Wilk and Levene's test statistics were both > 0.05 . Statistically significant differences between sampled populations were assessed with t-tests or ANOVA. Alpha level for all tests of statistical significance was 0.05. Individual means were compared following significant ANOVAs using Tukey's HSD post hoc test. Variables that did not meet the assumptions for parametric statistics were assessed with nonparametric methods of analysis. ANOVA's were replaced with Kruskal-Wallis tests and t-tests were replaced with Wilcoxon Signed Ranks tests. Pearson's correlations were used to look for relationships between factors.

Results

Tower Fire

Six plots were measured both before (Pre1 and Pre2) and after (Post) the fire. Results presented here are changes in the herbaceous community between the two pre-fire years and each pre-fire year to the post-fire year respectively. There were 78 total species identified among all three years (Table 1), with only one exotic species occurrence, *Lactuca serriola* (prickly lettuce) in Pre2. Seven species were unique to post-fire conditions, and 12 species were unique to pre-fire conditions (Tables 3 and 4). There was no significant change in canopy cover at the site since the fire remained on the ground. Mean and standard error statistics for species richness, relative frequency, and diversity for each year are presented in Table 5.

Multivariate repeated measures analyses and Kruskal-Wallis tests were carried out to test for a significant wildfire effect. The repeated measures analysis showed a significant difference in species richness between the three years ($p = 0.044$) (Figure 3). However, between year differences in species frequency and diversity were not significant (Figure 4).

Comparison within the Two Pre-fire Years:

Species richness increased, but not significantly, between pre-fire years (Figure 3). Seven species were found to be unique to 2000 and eight species were unique to 2001. Linear regression analysis showed that species richness and diversity were positively correlated ($r = 0.9105$, $p < 0.0116$) for Pre1, but not for Pre2. Species percent relative frequency was positively correlated with canopy cover for both Pre1 ($r = 0.8459$, $p < 0.034$) and Pre2 ($r = 0.9345$, $p < 0.0063$). However, there was not a significant correlation between species percent relative frequency and diversity. We did not find any correlations between the herbaceous variables and duff depth for Pre-fire conditions. There was a positive correlation between species diversity and litter depth for Pre1 ($r = 0.834$, $p < 0.0392$). Since basal area remained equal across all years, correlation analysis was not performed using this variable.

Comparison of Pre- and Post-fire Years:

Species richness was greater after the fire when compared to pre-fire years, but the difference was not significant (Figure 3). Neither species percent relative frequency nor diversity was found to be significantly

different before and after the fire (Figure 4). Linear regression analysis showed that species richness was positively correlated between both pre-fire years and Post (Pre1: $r = 0.9257$, $p < 0.008$ and Pre2: $r = 0.9261$, $p < 0.002$). Percent relative frequency was also positively correlated between Pre2 and Post ($r = 0.9757$, $p < 0.009$), with no correlation between Pre1 and Post. Species diversity was not significantly correlated for pre and post-fire years.

There was no significant correlation between forest floor (duff) and species richness, diversity, or relative frequency. Since basal area remained equal across all years, correlation analysis was not performed using this variable.

Post-fire Analysis:

Seven species were unique to the post-fire environment. Correlation analysis showed a significant relationship between post fire percent relative frequency and diversity ($r = 0.94419$, $p < 0.0157$). There was no relationship between post-fire richness and diversity. There was also a positive correlation between post-fire species percent relative frequency and canopy cover ($r = 0.871$, $p < 0.024$), and no relationship between richness and canopy cover. We did not find any correlations between the herbaceous variables and litter or duff depth for post-fire conditions.

Leroux Fire

Sixteen plots were measured both before and after the Leroux fire. There were 122 total species identified for both years (Table 2). Fourteen species were unique after the Leroux fire. Of these, the only new exotic species was *Cirsium vulgare* (bull thistle). Mean and standard error statistics for species richness, relative frequency, and diversity for each year are presented in Table 6.

There was an increase in exotic species richness after the fire (Wilcoxon Signed Ranks test, $Z = -2.072$, $p = 0.04$), but pre-fire and post-fire exotic species richness were not correlated. There was no significant difference in native species richness or overall species richness after the fire (Figure 5). Total species percent relative frequency decreased by half after the fire ($t_{(15)} = -4.51$, $p < 0.01$) (Figure 6). Species diversity decreased after the fire ($t_{(15)} = -3.61$, $p < 0.01$) (Figure 6). Unsurprisingly, there was a decrease in canopy cover after the fire ($t_{(15)} = -3.21$, $p = 0.01$).

We found that there was a positive correlation between pre-fire species diversity and plant percent relative frequency before the fire ($r = 0.57$, $p = 0.02$). Exotic species richness was also positively correlated with total richness before the fire ($r = 0.614$, $p < 0.01$). There was also a negative correlation between native species richness and canopy cover ($r = -0.55$, $p = 0.03$). Neither of these correlations was apparent in the post-fire data. After the fire there was a negative correlation between exotic species richness and total plant percent relative frequency ($r = -0.71$, $p < 0.01$). No correlation was found between the herbaceous variables and litter depth, duff depth, and percent overstory mortality for Pre or Post-fire conditions.

Discussion

Direct comparison of results between these two fires is not appropriate due to differences in sample size, sample period, and fire behavior. Given this, there are still some differences in trends that are worth noting. Fire increased exotic species richness at the Leroux fire, but not at the Tower fire. This is likely explained by the pre-fire existence of exotic species at the Leroux site coupled with increased levels of anthropogenic disturbances and propagule pressure. Species relative frequency and diversity did not change significantly after the Tower fire, while both decreased after the Leroux fire. We hypothesize that this variable response is due to differences in severity of the two fires, though our data can not exclude precipitation as a variable. This hypothesis is supported by the negative relationship between species relative frequency and percent overstory mortality in the Leroux fire. Unique species occurred in the post-fire environment of both fires, suggesting that fire is an important factor determining understory composition. From results of the Tower fire we also see that precipitation changed understory composition, evidenced by the unique species present in each of the two pre-fire years.

Analysis of species nativity within post-fire communities is confounded by the difficult identification of certain species. There is considerable uncertainty in literature concerning accurate identification of *Chenopodium album* and other broad-leaved *Chenopodium* species. There are five varieties of *C. album* in the USA, of which 3 are native and 2 are exotic. The *C. album* var. *album* is the only exotic considered to occur in Arizona and our study areas. Previously, *C. album* and *C. berlandieri* have been considered as distinct species (Kearney and Peebles 1960), or as varieties of *C. album* (Ruas et al. 1999). With all vegetative characteristics being identical the species are differentiated only by seed morphology and degree of pericarp adhesion (Kearney and Peebles 1960). Ruas et al (1999) demonstrated that there is a 90% genetic similarity between the species, and argued that there is no basis for separating the species. However, the varieties used in the study are unknown and the degree of similarity due to hybridization is also unknown. The classification of *C. album* as native or exotic can greatly influence the findings in a post-fire study because of its frequent and dense presence after fires. For example, Crawford et al. (2001) considered *C. Album* as an exotic species, resulting in 23 exotic species and 59% cover in the moderate burn, and 26 exotic species and 116% cover in the high burn. If *C. album* had not been considered an exotic the number of exotics would be reduced to 22 species and 48% cover in the moderate burn, and 25 species and 77% in the high burn. Due to the difficult or impossible distinction of these taxa under field conditions, we chose to combine these species at the genera level (referred to as *Chenopodium spp.*). We also chose to conservatively classify *Chenopodium spp.* as native, and not exotic for all analyses.

Tower Fire

While differences in species richness were not statistically significant between any years, the actual difference between the two pre-fire years was greater than between pre-fire years and post-fire. This trend may suggest that precipitation differences had an equivalent or greater effect on understory richness compared to the fire. Alternatively, the apparent lack of effect on understory richness due to fire could actually be due to the severe drought conditions. For example, the same fire occurring in a non-drought period could have produced dramatically different results. In this study we did not have control (unburned) plots in which to observe understory change due to climactic factors. Therefore, our study can not rule out non-fire variables and further investigation is needed to tease apart climactic and fire effects within this southwestern system. It is likely that both climate and fire were individual agents for change in this system, and possibly a third unmeasured climate-fire interaction effect occurred that is distinctly different from either effect individually.

Results did not show an increase in exotic species presence after the fire, even with one recorded occurrence prior to the fire. This indicates either that sufficient propagule pressure was lacking in order for exotics to become established or other community or environmental factors prevented increased establishment.

Leroux Fire

As with the Tower fire, species richness did not differ significantly between years, as we had hypothesized. We did not have unburned (control) plots in which to observe understory change due to climactic factors. Without control plots it is not possible to determine if this lack of change in species richness was due to fire or drought effect. The significant relationship found between species diversity and relative frequency highlights the important role of understory biodiversity in the ecosystem.

Davis et al. (2000) hypothesized that native and exotic species distributions are governed by the same factors. Our research showed that pre-fire exotic richness and total richness are positively correlated, and that post-fire exotic richness and native frequency were negatively correlated, which supports this hypothesis. Our study also agrees with other studies which have noted that exotic species are more likely to invade areas of high biodiversity (Stohlgren et al. 1999, 2001). Since high biodiversity areas are often important conservation targets, this emphasizes the importance of monitoring such areas for exotic species so that invasive plants can be removed before they become a problem. Previous research has also linked exotic species with anthropogenic disturbances such as roads and campgrounds (Sieg et al. 2003). The San Francisco Peaks are currently protected from many destructive disturbances (logging, off road vehicles) within the Kachina Peaks Wilderness Area, but are subject to frequent day and overnight use.

Plant communities are most vulnerable to invasion by exotic species when unused resources increase (Davis et al. 2000). Fire can increase unused resources by removing cover of perennial vegetation, increasing

nutrient availability, and increasing light availability by removing canopy cover. One year after the Leroux fire we noticed decreases in plant abundance and canopy cover. Decreases in plant abundance are most likely due to removal of perennial native vegetation. We completed our remeasurements of the plant community in the spring. Over the summer there was rapid plant growth in the burned area. Had we remeasured the plots later in the summer, we believe there would have been an increase in plant abundance. Fire has already been shown to disproportionately increase exotic species richness and abundance in this area relative to increases in native species (Crawford et al. 2001). In agreement with these results, we found the Leroux fire increased exotic species richness, with no accompanying change in native species richness. If this trend continues, this could create a cascade in which exotic species facilitate the invasion of other exotic species.

Conditions created by fire exclusion over the last hundred years include greater canopy closure and tree encroachment on meadows (Covington and Moore 1994, Moore and Huffman 2004). Much of the herbaceous vegetation survives poorly with the decreased light availability. Native plants which are adapted to frequent, low-intensity fire may become rare without the disturbance that sustains them. When fire does occur, the dense stands of young trees, increased fuel loads, and greater vertical fuel continuity can result in higher intensity fires to which the native plants may not be adapted (Moore et al. 2006). But, as discussed above, fire changes light and nutrient availability while removing competition from existing vegetation, creating ideal conditions for invasion (Davis et al. 2000). We saw no correlation between exotic species richness before and after the fire, indicating the fire provided opportunities for exotic species existing only in the seed bank before the fire.

Conclusions

Post-fire vegetation communities are greatly influenced by the pre-fire community, land-use history, and the response of exotic species. In agreement with Crawford et al. (2001) and Griffis et al. (2001), exotic species richness and frequency increased after fire when there was a significant exotic species presence prior to the fire. Exotic species richness increased with total biodiversity, supporting the invasion theory of Stohlgren et al. (1999 and 2001), but also decreased with native frequency, supporting common theory that high rates of native species establishment can reduce exotic establishment.

Precipitation and fire are two key agents in creating and maintaining understory communities in the southwestern ponderosa pine forest. In a severe drought period, as Northern Arizona is currently experiencing, it is possible for climatic factors to obscure or limit fire effects on the understory community. Understanding how the interaction between these two environmental factors affects the understory community and in turn affects conclusions of post-fire vegetation studies is crucial. Management decisions, such as, restoration, revegetation, and weed control are often based on studies addressing the effects of fire on the understory community. In the Southwest, where vegetation is highly affected by annual precipitation variation and longer term droughts, sampling multiple pre-fire years may provide a more reliable basis for comparison of post-fire data by incorporating the climactic variability of those years.

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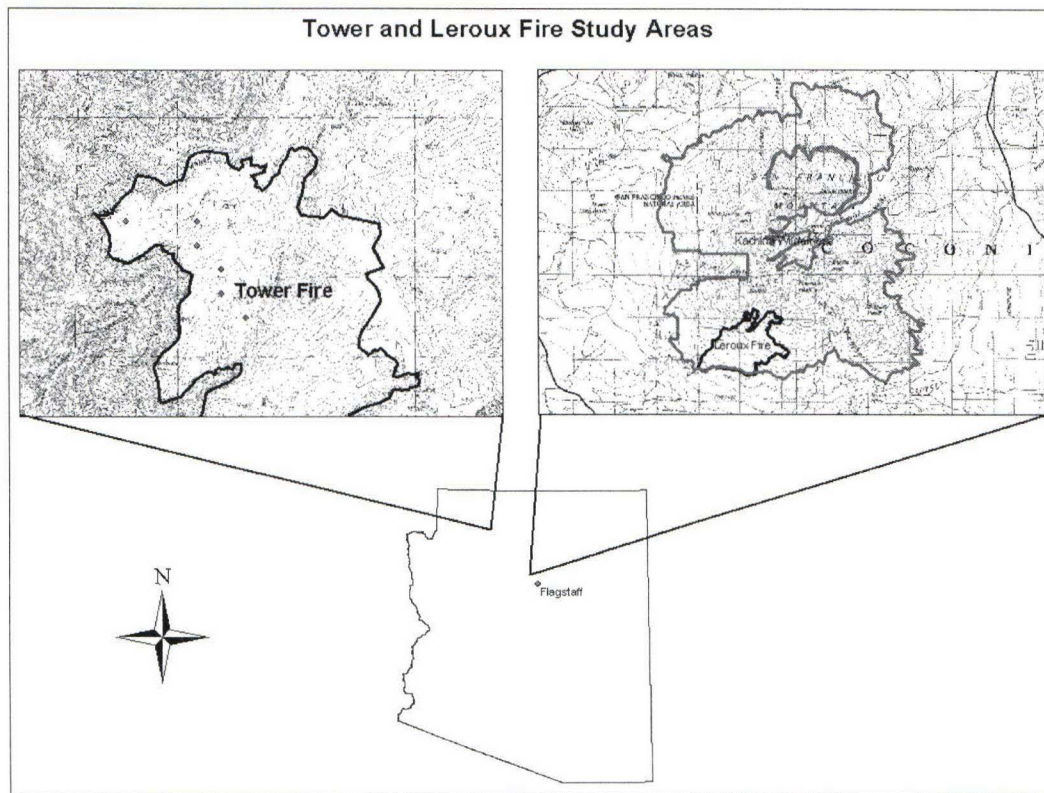


Figure 1. Grand Canyon (Tower Fire) and San Francisco Peaks (Leroux Fire) study areas.

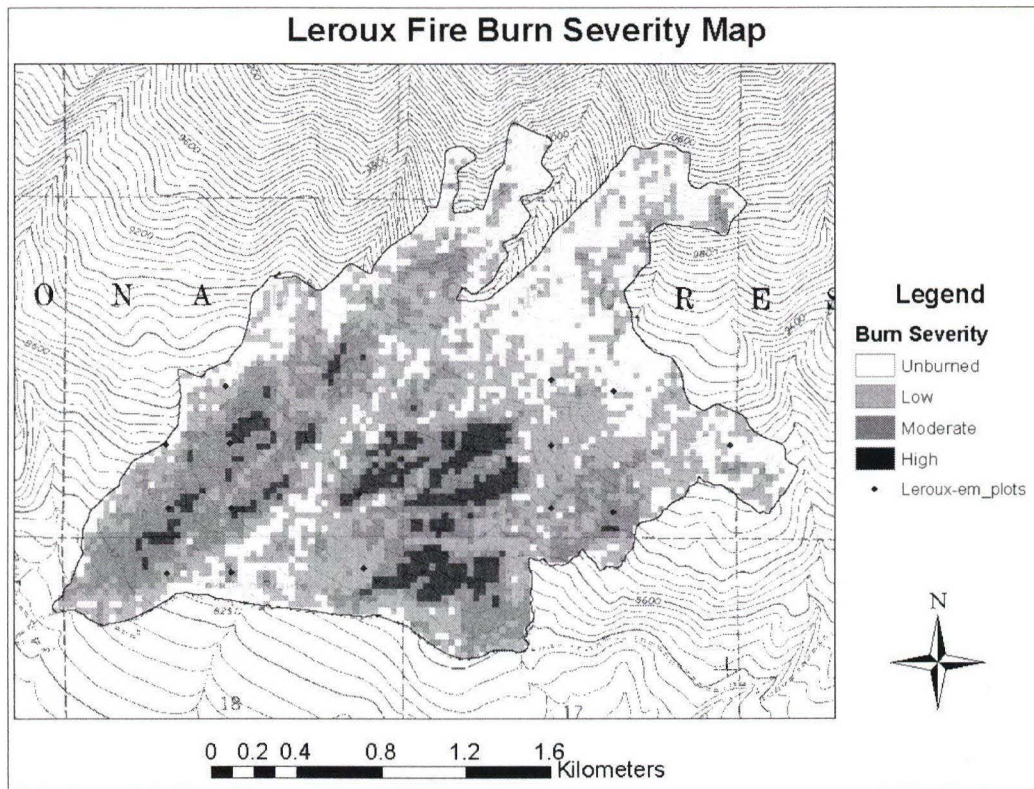


Figure 2. Leroux fire burn severity map with study plots.

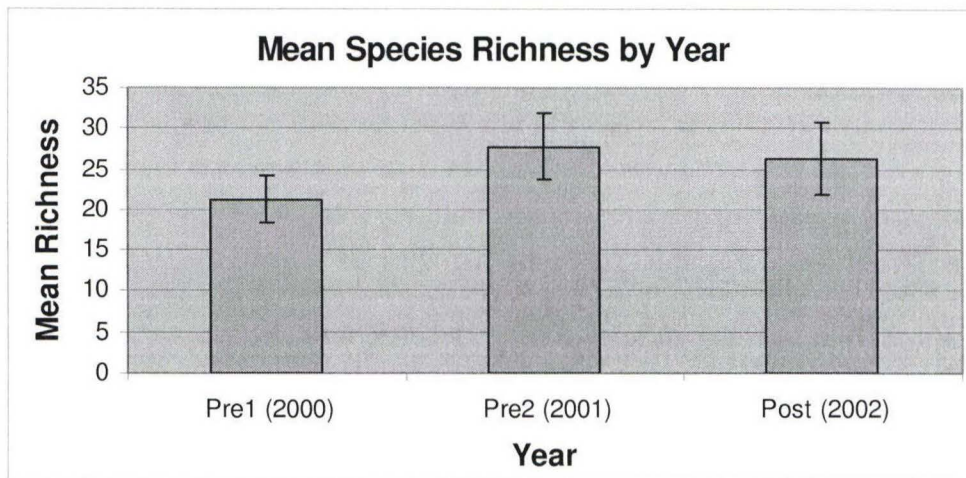


Figure 3. Tower fire comparison of mean species richness per year.

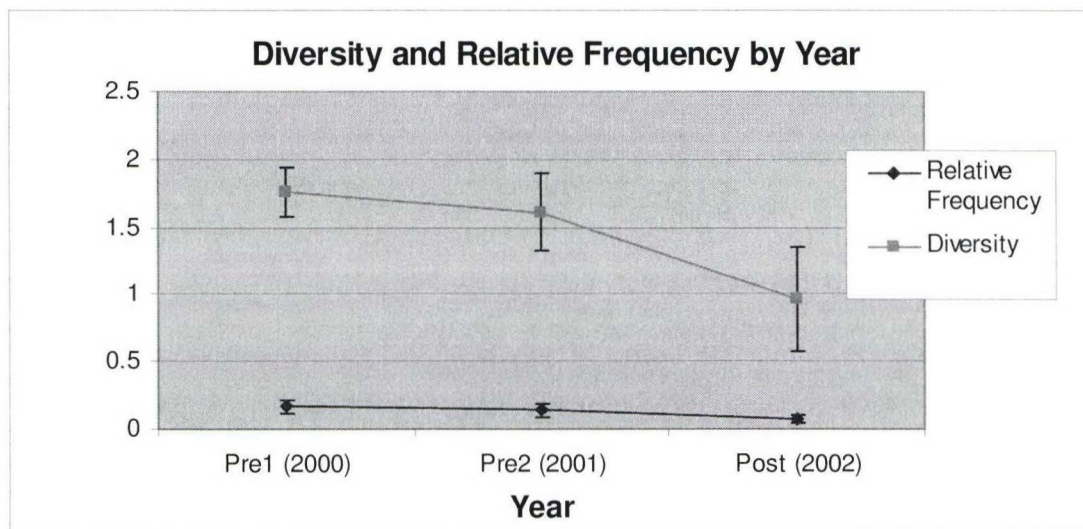


Figure 4. Tower fire comparison of mean species diversity and relative frequency by year.

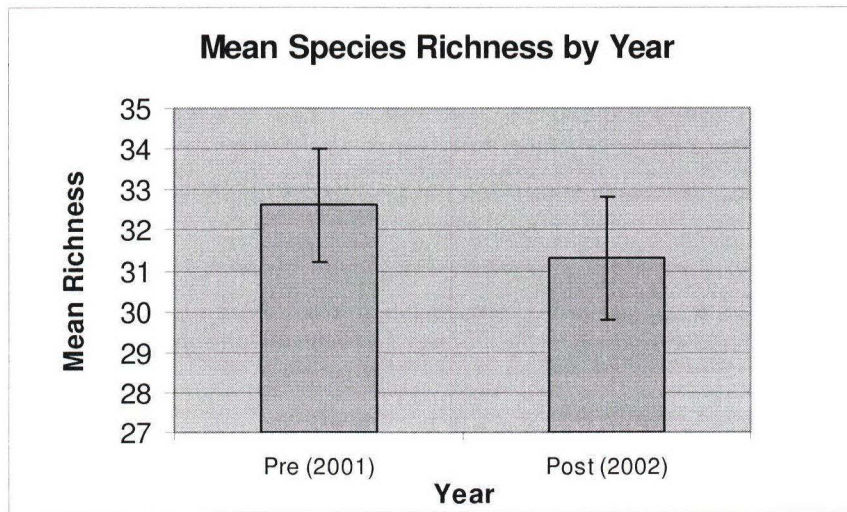


Figure 5. Leroux fire comparison of mean species richness per year.

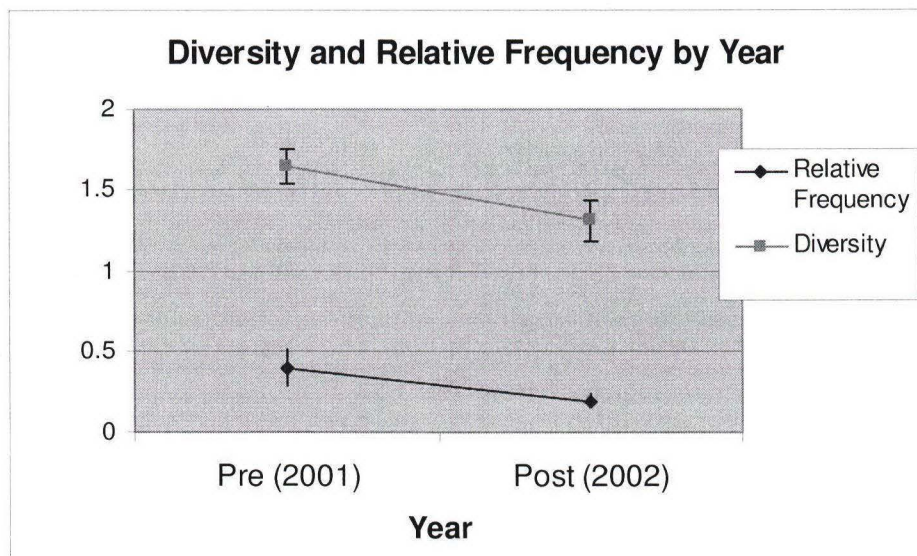


Figure 6. Leroux fire comparison of mean species diversity and relative frequency by year.

Table 1. Master species list and origin for Tower fire plots, all years included.

N = native, E = exotic, U = unknown

Genus	Species	Family	Origin	Growth Habit
Abies	concolor	Pinaceae	N	Tree
Achillea	millefolium	Asteraceae	N	Forb
Agoseris	glauca	Asteraceae	N	Forb
Amelanchier	utahensis	Rosaceae	N	Shrub
Antennaria	marginata	Asteraceae	N	Forb
Antennaria	parvifolia	Asteraceae	N	Forb
Arabis	sp.	Brassicaceae	U	Forb
Arenaria	lanuginosa ssp. saxosa	Caryophyllaceae	N	Forb
Astragalus	castaneiformis	Fabaceae	N	Forb
Blepharoneuron	tricholepis	Poaceae	N	Graminoid
Bromus	ciliatus	Poaceae	N	Graminoid
Bromus	ciliatus	Poaceae	N	Graminoid
Calochortus	nuttallii	Liliaceae	N	Forb
Carex	geophila	Cyperaceae	N	Graminoid
Carex	incurviformis	Cyperaceae	N	Graminoid
Carex	occidentalis	Cyperaceae	N	Graminoid
Carex	rosii	Cyperaceae	N	Graminoid
Ceanothus	fendleri	Rhamnaceae	N	Shrub
Chenopodium	album	Chenopodiaceae	N	Forb
Chenopodium	leptophyllum	Chenopodiaceae	N	Forb
Cirsium	sp.	Asteraceae	N	Forb
Cirsium	wheeleri	Asteraceae	N	Forb
Collinsia	parviflora	Scrophulariaceae	N	Forb
Comandra	umbellata	Santalaceae	N	Forb
Delphinium	nuttallianum	Ranunculaceae	N	Forb
Elymus	elymoides	Poaceae	N	Graminoid
Ericameria	nauseosa	Asteraceae	N	Shrub
Eriogonum	collinum	Polygonaceae	N	Forb
Erigeron	divergens	Asteraceae	N	Forb
Erigeron	flagellaris	Asteraceae	N	Forb
Erigeron	speciosus	Asteraceae	N	Forb
Eriogonum	racemosum	Polygonaceae	N	Forb
Fragaria	virginiana	Rosaceae	N	Forb
Gayophytum	diffusum ssp. parviflorum	Onagraceae	N	Forb
Gayophytum	diffusum ssp. parviflorum	Onagraceae	N	Forb
Geranium	caespitosum	Geraniaceae	N	Forb
Geranium	richardsonii	Geraniaceae	N	Forb
Goodyera	oblongifolia	Orchidaceae	N	Forb
Heliomeris	multiflora	Asteraceae	N	Forb
Heterotheca	villosa	Asteraceae	N	Forb
Hieracium	fendleri	Asteraceae	N	Forb
Kelloggia	galioides	Rubiaceae	N	Forb
Koeleria	macrantha	Poaceae	N	Graminoid
Lactuca	serriola	Asteraceae	E	Forb
Lithophragma	tenellum	Saxifragaceae	N	Forb
Lithospermum	multiflorum	Boraginaceae	N	Forb
Lomatium	foeniculaceum	Apiaceae	N	Forb

Lomatium	nevadense	Apiaceae	N	Forb
Lotus	utahensis	Fabaceae	N	Forb
Lotus	wrightii	Fabaceae	N	Forb
Lupinus	argenteus	Fabaceae	N	Forb
Lupinus	hillii	Fabaceae	N	Forb
Machaeranthera	gracilis	Asteraceae	N	Forb
Mahonia	repens	Berberidaceae	N	Subshrub
Packera	multilobata	Asteraceae	N	Forb
Paxistima	myrsinites	Celastraceae	N	Subshrub
Pedicularis	centranthera	Scrophulariaceae	N	Forb
Penstemon	barbatus	Scrophulariaceae	N	Forb
Penstemon	virgatus	Scrophulariaceae	N	Forb
Phacelia	egena	Hydrophyllaceae	N	Forb
Pinus	ponderosa	Pinaceae	N	Tree
Poa	fendleriana	Poaceae	N	Graminoid
Polygonum	douglasii	Polygonaceae	N	Forb
Polygonum	douglasii	Polygonaceae	N	Forb
Populus	tremuloides	Salicaceae	N	Tree
Pseudocymopterus	montanus	Apiaceae	N	Forb
Pseudotsuga	menziesii	Pinaceae	N	Tree
Pteridium	aquilinum	Dennstaedtiaceae	N	Fern
Quercus	gambelii	Fagaceae	N	Tree
Robinia	neomexicana	Fabaceae	N	Tree
Rosa	woodsii	Rosaceae	N	Shrub
Sambucus	nigra ssp. caerulea	Caprifoliaceae	N	Tree
Senecio	wootonii	Asteraceae	N	Forb
Silene	scouleri	Caryophyllaceae	N	Forb
Solidago	sp.	Asteraceae	N	Forb
Solidago	velutina	Asteraceae	N	Forb
Symphoricarpos	oreophilus	Caprifoliaceae	N	Shrub
Thalictrum	fendleri	Ranunculaceae	N	Forb
Thlaspi	montanum	Brassicaceae	N	Forb

Table 2. Master species list and origin for Leroux fire plots, all years included.

N = native, E = exotic, U = unknown

Genus	Species	Family	Origin	Growth Habit
Achillea	millefolium	Asteraceae	N	Forb
Agastache or	pallidiflora or	Lamiaceae	N	Forb
Dracocephalum	parviflorum			
Agoseris	glauca	Asteraceae	N	Forb
Androsace	septentrionalis	Primulaceae	N	Forb
Antennaria	parvifolia	Asteraceae	N	Forb
Antennaria	rosulata	Asteraceae	N	Forb
Arabis	sp.	Brassicaceae	N	Forb
Arabis	fendleri	Brassicaceae	N	Forb
Arceuthobium	sp.	Viscaceae	N	Shrub
Arenaria	lanuginosa	Caryophyllaceae	N	Forb
	ssp. saxosa			
Artemisia	carruthii	Asteraceae	N	Forb
Artemisia	ludoviciana	Asteraceae	N	Forb
Unknown	Asteraceae	Asteraceae	U	Unknown
Astragalus	humistratus	Fabaceae	N	Forb
Astragalus	sp.	Fabaceae	N	Forb
Astragalus	rusbyi	Fabaceae	N	Forb
Blepharoneuron	tricholepis	Poaceae	N	Graminoid
Brickellia	grandiflora	Asteraceae	N	Forb
Bromus	anomalus	Poaceae	N	Graminoid
Bromus	ciliatus	Poaceae	N	Graminoid
Bromus	inermis	Poaceae	E	Graminoid
Bromus	sp.	Poaceae	N	Graminoid
Bromus	tectorum	Poaceae	E	Graminoid
Calochortus	nuttallii	Liliaceae	N	Forb
Carex	sp.	Cyperaceae	N	Graminoid
Carex	geophila	Cyperaceae	N	Graminoid
Carex	occidentalis	Cyperaceae	N	Graminoid
Carex	petasata	Cyperaceae	N	Graminoid
Carex	rossii	Cyperaceae	N	Graminoid
Castilleja	sp.	Scrophulariaceae	N	Forb
Ceanothus	fendleri	Rhamnaceae	N	Shrub
Chenopodium	album	Chenopodiaceae	N	Forb
Chenopodium	capitatum	Chenopodiaceae	N	Forb
Chenopodium	sp.	Chenopodiaceae	U	Forb
Cirsium	sp.	Asteraceae	U	Forb
Cirsium	vulgare	Asteraceae	E	Forb
Cirsium	wheeleri	Asteraceae	N	Forb
Conyza	canadensis	Asteraceae	N	Forb
Corydalis	aurea	Fumariaceae	N	Forb
Echeandia	flavescens	Liliaceae	N	Forb
Elymus	elymoides	Poaceae	N	Graminoid
Epilobium	brachycarpum	Onagraceae	N	Forb
Erigeron	divergens	Asteraceae	N	Forb
Erigeron	flagellaris	Asteraceae	N	Forb
Erigeron	formosissimus	Asteraceae	N	Forb
Erigeron	sp.	Asteraceae	N	Forb
Erigeron	speciosus	Asteraceae	N	Forb
Euphorbia	sp.	Euphorbiaceae	N	Forb
Festuca	arizonica	Poaceae	N	Graminoid
Fraseria	speciosa	Gentianaceae	N	Forb

Geranium	caespitosum	Geraniaceae	N	Forb
Geum	triflorum	Rosaceae	N	Forb
Hieracium	fendleri	Asteraceae	N	Forb
Holodiscus	sp.	Rosaceae	N	Shrub
Houstonia	wrightii	Rubiaceae	N	Forb
Hymenoxys	hoopesii	Asteraceae	N	Forb
Hymenoxys	richardsonii	Asteraceae	N	Forb
	var. floribunda			
Iris	missouriensis	Iridaceae	N	Forb
Koeleria	macrantha	Poaceae	N	Graminoid
Lactuca	serriola	Asteraceae	E	Forb
Laennecia	schiedeana	Asteraceae	N	Forb
Lappula	occidentalis	Boraginaceae	N	Forb
Lathyrus	lanszwertii	Fabaceae	N	Forb
	var.			
	leucanthus			
Lathyrus/Vicia	sp.	Fabaceae	N	Forb
Lepidium	sp.	Brassicaceae	N	Forb
Unknown	Liliaceae	Liliaceae	U	Forb
Linaria	dalmatica	Scrophulariaceae	E	Forb
Linum	lewisii var.	Linaceae	N	Forb
	lewisii			
Lithospermum	sp.	Boraginaceae	N	Forb
Lithospermum	multiflorum	Boraginaceae	N	Forb
Lotus	sp.	Fabaceae	N	Forb
Lotus	wrightii	Fabaceae	N	Forb
Lupinus	argenteus	Fabaceae	N	Forb
Lupinus	kingii	Fabaceae	N	Forb
Mahonia	repens	Berberidaceae	N	Subshrub
Maianthemum	stellatum	Liliaceae	N	Forb
Mertensia	franciscana	Boraginaceae	N	Forb
Mirabilis	decipiens	Nyctaginaceae	N	Forb
Muhlenbergia	montana	Poaceae	N	Graminoid
Muhlenbergia	virescens	Poaceae	N	Graminoid
Muhlenbergia	wrightii	Poaceae	N	Graminoid
Oenothera	sp.	Onagraceae	N	Forb
Oxytropis	lambertii	Fabaceae	N	Forb
Packera	multilobata	Asteraceae	N	Forb
Penstemon	barbatus	Scrophulariaceae	N	Forb
Penstemon	linarioides	Scrophulariaceae	N	Forb
Pennellia	longifolia	Brassicaceae	N	Forb
Penstemon	virgatus	Scrophulariaceae	N	Forb
Phleum	pratense	Poaceae	N	Graminoid
Pinus	edulis	Pinaceae	N	Tree
Pinus	flexilis	Pinaceae	N	Tree
Pinus	ponderosa	Pinaceae	N	Tree
Poa	fendleriana	Poaceae	N	Graminoid
Populus	tremuloides	Salicaceae	N	Tree
Potentilla	crinita	Rosaceae	N	Forb
Potentilla	hippiana	Rosaceae	N	Forb
Potentilla	subviscosa	Rosaceae	N	Forb
Pseudognaphalium	macounii	Asteraceae	N	Forb
Pseudotsuga	menziesii	Pinaceae	N	Tree
Pteridium	aquilinum	Dennstaedtiaceae	N	Fern
Ribes	cereum	Grossulariaceae	N	Shrub
Ribes	sp.	Grossulariaceae	N	Shrub

Rosa	woodsii	Rosaceae	N	Shrub
Rubus	sp.	Rosaceae	U	Shrub
Sanguisorba	minor	Rosaceae	E	Forb
Schizachyrium	scoparium	Poaceae	N	Graminoid
Senecio	sp.	Asteraceae	N	Forb
Senecio	eremophilus	Asteraceae	N	Forb
Senecio	spartioides	Asteraceae	N	Forb
Silene	sp.	Caryophyllaceae	N	Forb
Solidago	sp.	Asteraceae	N	Forb
Symphoricarpos	oreophilus	Caprifoliaceae	N	Shrub
Taraxacum	officinale	Asteraceae	E	Forb
Thalictrum	fendleri	Ranunculaceae	N	Forb
Thermopsis	montana var. montana	Fabaceae	N	Forb
Thlaspi	montanum	Brassicaceae	N	Forb
Tragopogon	dubius	Asteraceae	E	Forb
Trifolium	longipes ssp. pygmaeum	Fabaceae	N	Forb
Unknown	Forb	Unknown	U	Unknown
Verbascum	thapsus	Scrophulariaceae	E	Forb
Vicia	americana	Fabaceae	N	Forb
Vicia	sp.	Fabaceae	N	Forb

Table 3. Tower fire: Number of species unique to each year.

Fire	# of Unique Species to Treatment			
	Pre1 (2000)	Pre2 (2001)	Post (2002)	Pre only
Tower Fire	4	6	7	12

Table 4. Tower fire: List of species unique to each year.

Genus	Presence Absence		Pre1	Pre2	Post
	Species				
Amelanchier	utahensis	X	X		
Arabis	sp.				X
Blepharoneuron	tricholepis	X	X		
Chenopodium	leptophyllum				X
Delphinium	nuttallianum			X	
Eriogonum	colomexicanus			X	
Eigeron	divergens	X			
Ericameria	nauseosa			X	
Heliomeris	multiflora	X			
Koeleria	macrantha				X
Lactuca	serriola			X	
Lithophragma	tenellum			X	
Lomatium	foeniculaceum				X
Lomatium	nevadense				X
Machaeranthera	gracilis				X
Paxistima	myrsinites	X			
Penstemon	virgatus				X
Sambucus	nigra ssp. caerulea	X			
Senecio	wootonii			X	

Table 5. Tower fire: Means and standard error for species richness, percent relative frequency, and diversity by year.

Variables	Pre1 (2000)	Pre2 (2001)	Post (2002)
Richness	21.17 +/- 2.93	27.83 +/- 4.09	26.33 +/- 4.40
Relative Frequency	0.163 +/- 0.051	0.139 +/- 0.049	0.064 +/- 0.028
Diversity (Shannons H')	1.76 +/- 0.184	1.61 +/- 0.284	0.965 +/- 0.396

Table 6. Leroux fire: Means and standard error for species richness, percent relative frequency, and diversity by year.

Variables	Pre (2001)	Post (2002)
Overall Richness	32.63 +/- 1.4	31.31 +/- 1.53
Relative Frequency	0.396 +/- 0.11	0.195 +/- 0.045
Diversity (Shannons H')	1.645 +/- 0.11	1.31 +/- 0.13

Appendix 2: Dalmation Toadflax Response to Wildfire and Native Species Revegetation in Ponderosa Pine Forest

DALMATIAN TOADFLAX (*LINARIA DALMATICA*) RESPONSE TO WILDFIRE
AND
NATIVE SPECIES REVEGETATION
IN PONDEROSA PINE FOREST

By Rita Suzanne Dodge

A Thesis

Submitted in Partial Fulfillment
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Approved:

Pete Z. Fule, PhD. Co-chair

Carolyn Hull Sieg, Ph.D.
Co-chair

Laura E. DeWald, Ph.D.

ABSTRACT

DALMATIAN TOADFLAX (*Linaria dalmatica*) RESPONSE TO WILDFIRE AND NATIVE SPECIES REVEGETATION IN PONDEROSA PINE FOREST

Rita Suzanne Dodge

Within the context of ecological restoration, the goal of this study was to assess disturbance, exotic species, and native plant revegetation in two complementary ways. The increased size of severe fires in recent years in the southwestern U.S. has created large patches of higher severity burns that are available for colonization and spread of invasive exotic species and may require revegetation. We measured (1) the response of Dalmatian toadflax growth and reproduction to varying burn severity; and (2) the impact of toadflax on the native understory community, for three years after a wildfire in the ponderosa pine forest of northern Arizona. Toadflax density, cover, and flower stalks increased in the second year, then declined slightly in the third year in each burn severity class, although all variables remained higher in the third year than in the first. Change in toadflax variables from 2002 to 2003 differed ($p < 0.001$) among fire severity classes, with the greatest increase on high severity plots. In contrast, change in toadflax variables from 2003 to 2004 only differed among toadflax density classes ($p < 0.001$). Although toadflax declined in plots by the third year, we found evidence of spread into previously uncolonized areas surrounding plots. Native species richness differed among burn severity classes, and was not correlated to toadflax density or cover. We recommend focusing control efforts on high and moderate burn severity areas. Toadflax variables increased the most in the low density class, therefore control efforts should be focused at the periphery of large patches or on new satellite population where density is low.

Revegetation is one of the most common and economically efficient practices to restore disturbed areas by increasing native species richness and abundance, and reducing exotic species invasion. The second study evaluated the germination and growth performance of 28 native southwestern species and one exotic grass species to indicate their success for accomplishing revegetation goals. We conducted three seed

performance trials in a germination chamber, a greenhouse, and in the field and developed an integrated relative species performance rating. Cool season grasses and forbs had higher average germination in all three trials and higher cover and biomass production during the first field season than warm season species. Grass germination was slightly higher than forbs in the field, but provided twice as much cover by the second field season. Species with the highest overall field performance ratings were squirreltail (*Elymus elymoides*), blue gramma (*Bouteloua gracilis*), purple locoweed (*Oxytropis lambertii*), and ragleaf bahia (*Bahia dissecta*). The exotic annual ryegrass (*Lolium multiflorum* var. *gulf*) did not perform better than native grasses or forbs in the field, therefore, we do not recommend not using this species over native grasses for revegetation in the southwestern U.S. We recommend a combination of cool and warm season grasses and forbs to provide plant cover all year and accomplish revegetation goals.

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TABLE OF CONTENTS

ABSTRACT.....	27
ACKNOWLEDGMENTS	29
TABLE OF CONTENTS.....	30
LIST OF TABLES	31
LIST OF FIGURES	33
PREFACE	34
 CHAPTER 1: INTRODUCTION	 35
 CHAPTER 2: LITERATURE REVIEW	 40
Introduction.....	40
Disturbance Influences Plant Communities.....	41
Impacts and Invasion of Exotic Species	42
Dalmatian Toadflax Life History.....	44
Dalmatian Toadflax Control	46
Policy	50
Revegetation with Native Species: Use and History	50
Native versus Exotic Species for Revegetation	53
Literature Cited	55
 CHAPTER 3: DALMATIAN TOADFLAX (LINARIA DALMATICA (L.) MILLER) RESPONSE TO WILDFIRE IN A SOUTHWESTERN PONDEROSA PINE FOREST	 62
Abstract	62
Introduction.....	63
Methods.....	66
Results.....	70
Discussion	73
Literature Cited	97
 CHAPTER 4: NATIVE SPECIES REVEGETATION: A SPECIES-BASED PERFORMANCE EVALUATION	 100
Abstract	100
Introduction.....	101
Methods.....	104
Results.....	110
Discussion	115
Literature Cited	142
 CHAPTER 5: MANAGEMENT IMPLICATIONS	 145

LIST OF TABLES

Table 3.1. Total number of plots in each burn severity by Dalmatian toadflax stem density class in 2002.	54
Table 3.2. List of plant species, by family, found in study plots during all three years, and information on nativity and life history strategy	80
Table 3.3. Means (S. E.) for Dalmatian toadflax stem density, percent cover, and flowering stalk density by burn severity and toadflax density class for three years post-fire.	86
Table 3.4. Summary of statistical tests of significance for Dalmatian toadflax stems, cover, and flowering stalks. Repeated measures was used to test for the year x burn severity x density interaction, followed by an ANOVA on the difference between years.	88
Table 3.5. Average (S. E.) native and exotic plant species richness by burn severity and toadflax density class for three years post-fire.	89
Table 3.6. Pearson's correlation coefficient (r) of native species richness between years and by burn severity class.	90
Table 3.7. Transition matrices of the probability (proportion) of plots changing toadflax stem density class from 2002 to 2004, by burn severity class: a) unburned, b) low burn severity, c) moderate burn severity, and d) high burn severity.....	91
Table 4. 1 List of plant species used in germination trials near Flagstaff, Arizona, and information on life form, life history strategy, photosynthetic pathway/growing season, and collection information	95
Table 4. 2 Total monthly precipitation (cm) and minimum and maximum temperatures (°C), compared to the long-term average (54 years) during the 2003 and 2004 growing seasons, in Flagstaff, Arizona (Western Regional Climate Center).	127
Table 4. 3. Macronutrient content for total nitrogen, phosphorous, potassium, magnesium, and calcium, plus organic matter content and pH of soil used in greenhouse and field germination tests of 29 plant species, in Flagstaff, Arizona.	127
Table 4. 4. Percentage germination (standard error) of 29 species, by family, in a germination chamber, plus percentage emergence in greenhouse and field trials in Flagstaff, Arizona, in 2003 and 2004.....	128
Table 4. 5. Average percent aerial and basal cover per individual plant, plus average height, shoot and root length, and number of flowering stalks (standard error) for 29 species, by family, in a greenhouse trial in Flagstaff, Arizona.	130

Table 4. 6. Average shoot and root biomass per individual plant, plus the root: shoot ratio (standard error) for 29 species, by family, in a greenhouse and first season (2003) field trial in Flagstaff, Arizona.....	132
Table 4.7. Average percent aerial and basal cover per plot, plus average height, shoot and root length (standard error) for 29 species, by family, in a first season field trial in Flagstaff, Arizona.	134
Table 4. 8. Average percent aerial and basal cover per plot, plus average height, shoot and root length, and number of flowering stalks (standard error) for 29 species, by family, in a second season field trial in Flagstaff, Arizona.....	136
Table 4.9. Above-ground biomass (standard error) production in the second growing season (2004) for 29 species, by family, in a field trial in Flagstaff, Arizona.....	138
Table 4.10. Relative species performance rating of 29 species, by photosynthetic pathway, for the field trial, including ratings for percent cover (2003 and 2004), total germination, total biomass (2003), shoot biomass (2004), and overall performance rating.	140

LIST OF FIGURES

Figure 1. Leroux fire burn severity map with Dalmatian toadflax monitoring plot locations.	92
Figure 2. The average number of Dalmatian toadflax stems per plot (m^2) for each year according to burn severity class, and results of Tukey's HSD comparing the rate of change between years. Lines labeled with the same letter are similar, and different letters indicate a statistical difference.	93
Figure 3. The average % cover of Dalmatian toadflax per plot (m^2) for each year according to burn severity class, and results of Tukey's HSD comparing the rate of change between years. Lines labeled with the same letter are similar, and different letters indicate a statistical difference.	93
Figure 4. The average number of Dalmatian toadflax flowering stalks per plot (m^2) for each year according to burn severity class, and results of Tukey's HSD comparing the rate of change between years. Lines labeled with the same letter are similar, and different letters indicate a statistical difference.	94
Figure 5. Average native species richness per plot (m^2) according to burn severity class, for each monitoring year.	94
Figure 6. Average exotic species richness per plot (m^2) according to burn severity class, for each monitoring year.	95
Figure 7. Chronologic photographs taken of the same plot which shows Dalmatian toadflax spread outside of the plot frame.	96

PREFACE

This thesis was written in manuscript format. It contains an introduction, comprehensive literature review, two journal manuscript chapters, and concludes with a management implications chapter. Methods are contained within each of the manuscript chapters. The result is some redundant material, which has been kept to a minimum. Species scientific names were taken primarily from the USDA Plants Database (2004) and classified as native or exotic to Arizona according to the *Arizona Flora* (Kearney and Peebles 1960).

CHAPTER 1

INTRODUCTION

Wildfire is the primary natural disturbance in ponderosa pine (*Pinus ponderosa*) forests of the southwestern U.S.; it has a profound influence on overstory structure and understory composition, and maintains ecosystem form and function (Covington & Moore, 1994b). Historically, frequent, fast moving surface fires occurred every 2-20 years in this region (Swetnam & Baisan, 1996), but recent changes in the historical fire regime have included a number of rare, but large, intense, stand-replacing wildfires (Covington & Moore, 1994a). Severe wildfires create areas of exposed mineral soil, with little to no vegetation and litter, high resource availability, and increased soil temperatures, which create opportunities for colonization by invasive, exotic plant species (Crawford *et al.*, 2001; Griffis *et al.*, 2001). Some exotic species abundance has been documented to increase in high burn severity areas in the ponderosa pine forest of northern Arizona (Crawford *et al.*, 2001; Griffis *et al.*, 2001).

A key mechanism for exotic species invasion is the availability of excess resources (Stohlgren *et al.*, 1999, Davis *et al.*, 2000; Swope, 2003), which can be made available after fire disturbances. Exotic species are the second leading cause for the listing of threatened endangered species in the U.S., with the first being loss of habitat (Stein *et al.* 2000). Worldwide, invasive exotic species have replaced native vegetation, displaced animals, out-crossed with native flora, altered nutrient-cycles, altered hydrology, altered disturbance regimes and other ecosystem functions (Walker & Smith, 1997; Vitousek *et al.*, 1997). Economically, exotic species have reduced wild and domestic livestock forage, commercial and recreational land value, lowered water tables, poisoned livestock, and impacted aesthetic values (Sheley & Petroff, 1999).

Dalmatian toadflax (*Linaria dalmatica* (L.) Miller) is an invasive, exotic species in the U.S. that was introduced into Canada as an ornamental plant from the Mediterranean region and is now found throughout the western U.S. and southwestern

Canada (Alex, 1962; Vujnovic & Wein, 1996). Toadflax can reduce native plant species richness, cover, and germination and, therefore, is credited with impacting ecosystem function (Robocker, 1974; Lajeunesse, 1999). Fire typically does not kill the deep roots of Dalmatian toadflax so the growth, reproduction and biomass of Dalmatian toadflax increases under post-fire conditions (Jacobs & Sheley, 2003). The leaves and stems of toadflax contain poisonous alkaloids; it is not consumed by wildlife or domestic livestock (Lajeunesse, 1999; Vujnovic & Wein, 1996). These characteristics of Dalmatian toadflax allow it to persist in an ecosystem for decades.

Areas disturbed by wildfire and other anthropogenic disturbances may require revegetation to assist in the recovery of the natural vegetation and reduce ecosystem damage and the potential for exotic species invasion (Barro & Conard, 1987; Robichaud *et al.*, 2000; Crawford *et al.*, 2001). Native species are preferred over introduced species for revegetation because they are more likely to be adapted to the local environment, have greater genetic variability, and have greater production to sustain populations for a long period (Richards *et al.*, 1998; Mortlock, 2000). The use of non-native species for revegetation has resulted in reduced native plant species germination and richness, monocultures, and land type conversion (Keeley *et al.*, 1981; Barro & Conard, 1987). Recent municipal, state, and federal legislation requires public land managers to use native species in revegetation projects (Richards *et al.*, 1998). However, there is little knowledge about how some native species perform when seeded, and how they compare to exotic species performance (Korb, 2001; Korb & Springer, 2003).

The goal of this study was to assess disturbance, exotics, and native plant revegetation in two complementary ways. First, we selected a severe wildfire site in northern Arizona to quantify the growth and reproduction response of Dalmatian toadflax at varying burn severity levels for three years post-fire. Additionally, we asked if toadflax negatively impacted the native plant community. Second, in a companion study, we conducted three growth performance trials on 28 native plant species that could be candidates for use in revegetation programs. We gathered data on growth chamber, greenhouse, and field germination and performance and developed an integrated relative

performance rating for these species. A non-native ryegrass (*Lolium multiflorum* var. *gulf*) was also included in the study to provide a comparison of native to this non-native performance.

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CHAPTER 2

LITERATURE REVIEW

This review discusses the role of fire as a disturbance agent in northern Arizona, impacts exotic species have on ecosystems and native flora, biology and ecosystem impacts of Dalmatian toadflax (*Linaria dalmatica* (L.) Miller), control of Dalmatian toadflax, revegetation history, and using native versus exotic species for revegetation.

Introduction

The herbaceous community of northern Arizona ponderosa pine forests is composed of a diverse array of native grasses and forbs, which maintain a crucial role in ecosystem structure, function, and processes (Korb & Springer, 2003). Prior to Euro-American settlement (circa 1870), wildfire was the primary natural disturbance influencing the understory community and reducing tree density with frequent, fast moving surface fires across the landscape (Covington & Moore, 1994b). Before Euro-American settlement the ponderosa pine forest was characterized as “park-like” with clusters of old growth pines separated by grassy meadows (Covington & Moore, 1994b). Presently, southwestern forests are overcrowded, have dense “dog-hair” thickets, thick pine needle accumulation, and closed canopy, which all act to block light to the forest floor and understory vegetation (Covington & Moore, 1994b). Under these conditions the understory composition has changed; there is less variety and abundance, and native seed banks have been depleted (Covington & Moore, 1994b; Springer, 1999). Overcrowded forests have also created conditions susceptible to large-scale, high intensity wildfires and exotic species invasion, which have created a need for native species revegetation.

Disturbance Influences Plant Communities

Disturbance plays an integral role in influencing plant communities and maintaining ecosystem form, function, and processes (Hobbs & Huenneke, 1992; Agee, 1993). Low to moderate disturbances can promote native species biodiversity (intermediate disturbance hypothesis) (Connell, 1978), while large scale or intense disturbances can be detrimental to many ecosystems (Hobbs & Huenneke, 1992). Many vegetation types are historically characterized by a specific disturbance regime, such as frequent surface fire in ponderosa pine forest, which acts to insure plant survival and biodiversity (Pickett & White, 1985). Overgrazing in the late 1800's led to fire exclusion and the 1910 federal fire suppression policy and forest management practices greatly reduced the role of natural fire disturbance in ponderosa pine ecosystems (Pyne, 1982; Covington & Moore, 1994b). This led to a shift in the fire regime from frequent surface fires recurring every 2-20 years (Swetnam & Baisan, 1996) to less frequent but intense, large scale crown fires occurring today (Covington & Moore, 1994a; Covington & Moore, 1994b; Swetnam *et al.* 1999). Many species in northern Arizona are adapted to a frequent fire regime and may be negatively impacted by fire exclusion and high-severity fires (Korb & Springer, 2003).

Currently, disturbance events such as fire, urban development, and recreation that affect vegetative communities throughout the range of ponderosa pine (*Pinus ponderosa*) have increased in extent, frequency, and severity (Covington & Moore, 1994b; Brown & Sieg, 1996; Fulé *et al.*, 1997; Covington *et al.*, 1997; Fulé *et al.*, 2001). When changes in a disturbance regime occur at a faster rate or larger scale than vegetation can recover from or adapt to through natural processes, ecosystem degradation can occur. Indications of degradation include soil erosion, alteration of soil attributes and nutrients, exotic species invasion, exotic out-crossing with native species, reduced native biodiversity, and reduced wildlife habitat. When the natural capabilities of an ecosystem to recover from disturbance are overwhelmed, human intervention in the form of exotic species control and revegetation may be required to accelerate the recovery process and reduce ecosystem degradation (Crawford *et al.*, 2001; Korb & Springer, 2003; Sieg *et al.* 2003).

Impacts and Invasion of Exotic Species

Invasive exotic plant species in general are detrimental to ecosystems worldwide because they have the potential to replace native vegetation, displace animals, out-cross with native flora, alter nutrient cycles, hydrology, and disturbance regimes, and affect other ecosystem functions (Walker & Smith, 1997; Vitousek *et al.*, 1997). Non-native species are the second greatest cause for the listing of endangered and threatened species in the U.S., with the most frequent cause being loss of habitat (Stein *et al.* 2000). Not all exotic species are invasive, but invasive exotic species are those that are able to successfully establish and reproduce at the expense of native species or natural ecosystem function (Vitousek *et al.* 1997). Invasive exotic species are often able to colonize and thrive in new habitats because of widespread dispersal mechanisms, high seed production, and long seed longevity, as well as the absence of natural predators, pathogens, or competing vegetation to control population growth (Sheley & Petroff, 1999). Some exotics are able to perpetuate their existence by inhibiting competing vegetation with allelopathic compounds (Callaway & Aschehoug, 2000), or changing fire regimes (D'Antonio & Meyerson, 2002). Many exotics have also been implicated in increasing soil erosion and controlling aspects of the biogeochemical cycle (D'Antonio & Meyerson, 2002). Economically, exotic species have reduced wild and domestic livestock forage, commercial and recreational land value, lowered accessible water tables, poisoned livestock, and impacted aesthetic values (Sheley & Petroff, 1999).

A key mechanism for exotic species invasion is excess resource availability (Stohlgren *et al.*, 1999; Swope, 2003). Two common measurements of the native community are 1) species diversity, which addresses the species composition based on life cycle, functional group, and family and 2) species richness, which is a simple count of species. Several studies have shown that areas of low species diversity and richness are more susceptible to exotic invasion than species-rich areas because the available resources are not being utilized completely by the native community (Elton, 1958;

Rejmanek', 1996; Tilman, 1997). However, even areas with high species diversity and richness can be successfully invaded if excess resource availability exists (e.g. riparian systems) (Stohlgren *et al.*, 1999; Stohlgren *et al.*, 2001). Disturbed areas can have an excess of resources such as light, water, nutrients, and growing space, which if not utilized by native species provide opportunities for establishment of non-native species, particularly burned areas.

Even though the scale of stand-replacing fires increased throughout the late twentieth century (Swetnam *et al.*, 1999), there is a lack of knowledge about understory vegetation recovery following intense large-scale fires in ponderosa pine forests of the southwest (Crawford *et al.*, 2001). Wildfires leave behind large areas of exposed mineral soil, sometimes devoid of vegetation and seeds, that are quickly colonized by both native and exotic seral opportunists (Bazzaz, 1986; Orians, 1986; Sieg *et al.*, 2003). Griffis *et al.* (2001) found that while most understory vegetation responded positively in disturbed areas, exotic species responded disproportionately well along a disturbance gradient in ponderosa pine forests in northern Arizona. Both Crawford *et al.* (2001) and Griffis *et al.* (2001) found post-fire increases in overall species richness due to the additional presence of exotic species, not natives. Both studies reported increased exotic abundance with increased burn severity and the greatest exotic species abundance and richness in high severity burn areas (Crawford *et al.*, 2001; Griffis *et al.*, 2001). The abundance of native forbs increased as disturbance severity increased up to a moderate level, but richness declined with increasing severity. Similarly, the abundance and richness of native graminoids increased up to moderate disturbance levels, but decreased drastically in the wildfire treatment (Griffis *et al.*, 2001). After the La Mesa Fire in New Mexico, forbs dominated the severely burned sites initially, but decreased over time (Foxx, 1994). Burned areas with remaining tree cover also had higher understory cover in the first years after the fire, but areas lacking tree canopy cover had greater understory cover in later years (Foxx 1994).

Some exotic species are able to change the fire regime itself, which alters nutrient composition and availability, and reduces native species abundance. Cheatgrass (*Bromus*

tectorum L.), an exotic annual grass, is a classic example of this phenomenon and is well known for changing fire regimes in western states by creating a feedback loop that enhances its own survival (Cione *et al.*, 2002; Brooks *et al.*, 2004).

Dalmatian Toadflax Life History

Dalmatian toadflax (*Linaria dalmatica* (L.) Miller), which is native to the Mediterranean region, is an exotic invasive species in the United States. Dalmatian toadflax was introduced to the southwestern region of Canada and northwestern U.S. in 1894 as an ornamental plant, where it continued to spread along the southern Canadian border and south to the western states in the U.S. (Alex, 1962; Jacobs & Sheley, 2003; Vujnovic & Wein, 1996). The earliest recorded collection in Flagstaff, Arizona was in 1940 by Chester Deaver on the Northern Arizona University campus (Deaver Herbarium).

Dalmatian toadflax is a short-lived perennial member of the Scrophulariaceae family, and its yellow flower resembles that of a common snapdragon. Reproduction is by sprouting from an extensive root system and by seed, although it is self-sterile. One plant was found to produce up to 500,000 seeds per ten mature stems, which can also remain viable for as long as ten years in the field in Washington (Robocker, 1970). Seeds are dispersed by animal fur and wind, although a study on *L. vulgaris* P.Mill. (common toadflax) found that 90% of the seeds fell immediately next to the parent plant (Nadeau & King, 1991). Dalmatian toadflax roots extend up to 3 m horizontally and 3 m vertically and contain large carbohydrate reserves. These reserves allow toadflax to be competitive with native winter annuals and to sprout earlier than natives in the spring (Robocker 1970, Lajeunesse 1999). No studies have shown this species to be allelopathic.

Our observations over the past 3 years in northern Arizona indicate that growth begins in mid-March continuing until the first freeze, and flowering occurs from mid-

May into October. Similar growth and flowering patterns have been observed in Washington (Robocker 1970, Alex 1962) and Montana (Lajeunesse, 1999). Dalmatian toadflax has been located up to 3050 m elevation on the San Francisco Peaks (Fisher & Fulé, 2004). Dalmatian toadflax differs from other perennial species because it retains prostrate, vegetative stems during the winter that aid in early spring sprouting of flowering stems. Dalmatian toadflax is adapted to a wide range of habitats, but favors well-drained, relatively coarse soils (Lajeunesse 1999).

Infestations of Dalmatian toadflax are potentially detrimental both ecologically and economically to rangelands and wildlands and it has become a successful invader in many locations in the United States. This species is designated as a “noxious weed” in Arizona and 11 other western states (USDA NRCS, 2004) and in 3 Canadian provinces (Rice, 2004). “Noxious” is a legal classification which places restrictions on the sale and transport of Dalmatian toadflax seeds and plants, as well as requiring control efforts. It is also considered a serious rangeland weed in Canada and the northwest U.S., where large infestations have replaced forage species for both domestic livestock and wildlife (Lajeunesse 1999, Vujnovic and Wein 1996). Dalmatian toadflax disrupts ecosystem composition and structure by replacing native plant species (Robocker, 1974; Lajeunesse, 1999; Grieshop & Nowierski, 2002) and even other weeds (Lange, 1958). Several toxic alkaloids are found in the leaves and stems of Dalmatian toadflax making it poisonous to wildlife and domestic livestock (Vujnovic 1996, Lajeunesse 1999). Sheep are the only animal observed grazing toadflax without experiencing detrimental effects (Lajeunesse, 1999). By replacing native vegetation, large infestations of toadflax could disrupt the grazing and migration patterns of ungulates. No research has directly addressed the effects of toadflax on small mammal populations, insects, soil microbes, and mycorrhizae that are associated with the native vegetation, though it is likely that any changes to these ecosystem components would reflect that of the displaced native vegetation.

There have also been no studies exploring the effects of toadflax on soil nutrient composition, hydrology, or soil erosion. However, it is known that the dominant bunch grasses in northern Arizona and other herbaceous species contribute nutrients, provide

food and cover for wildlife, carry low-severity ground fires, and have fibrous root systems that hold soil in place and maintain mycorrhizal communities (Korb & Springer, 2003). In contrast, toadflax has a taproot system rather than fibrous roots. Taproots generally do not hold soil as well but allow increased access to water. An additional problem associated with Dalmatian toadflax is that it thrives in disturbed environments such as roadsides, construction areas, and trails and it is able to resprout repeatedly when top-growth is removed (Lajeunesse 1999).

Dalmatian toadflax is fire-adapted in that it establishes quickly after, and growth is enhanced by fire, but it has not been found to alter fire regimes. Only one study in the U. S. has been published on the response of toadflax to fire. Jacobs and Sheley (2003) found that prescribed fire increased Dalmatian toadflax plant biomass, and dramatically increased seed production, between 2 and 50 times. The cover of toadflax in burned plots also increased; however, it was not significantly different from the change in the unburned plots (Jacobs & Sheley, 2003). On the Coconino National Forest researchers studying the sensitive species Flagstaff pennyroyal (*Hedeoma diffusum* Greene), found that a population was invaded by Dalmatian toadflax after prescribed burning (Phillips & Crisp, 2001). Dalmatian toadflax was present in areas adjacent to the study area before the burning and study plots burned prior to the onset of summer rains (June) were invaded by Dalmatian toadflax, while plots burned after the onset of the rainy season (July) were not invaded.

Dalmatian Toadflax Control

Most of the research on Dalmatian toadflax has focused on control rather than the physiological and biological attributes of the species. A variety of techniques and combinations thereof have been used to control Dalmatian toadflax and restore native vegetation including: manual pulling, mechanical removal (e.g. mowing), chemical, and biocontrol. Toadflax is very persistent due to its large carbohydrate reserves, extensive root system, and resprouting ability. Therefore, it is imperative to repeat control

treatments for several years or multiple times within a season regardless of the method used (Lajeunesse, 1999; Vujnovic & Wein, 1996). It is ideal to conduct any treat method prior to flowering rather than seed set to prevent the pollination of other populations not being treated. It is possible that a winter treatment to remove vegetative stems may have a significant impact on growth the following season, though no studies have thoroughly addressed the timing of treatment (Robocker, 1974). All treatments must be repeated annually for 5-6 years to remove plants, and 10-15 years to remove seedlings that sprout from the seed bank (Lajeunesse *et al.*, 1993; Lajeunesse, 1999).

Manual pulling is the easiest and least expensive method for small infestations, and is the easiest way to involve volunteers in a control project. Another advantage of pulling is that it addresses both seed set and vegetative spread, which are keys for successful treatment (Lajeunesse, 1999). Pulling in spring after the mature stems have sprouted and prior to flowering or seed set may reduce carbohydrate reserves (Robocker *et al.*, 1972). Pulling should be repeated throughout the season before seed set (Lajeunesse, 1999).

Mechanical methods such as mowing or clipping are not recommended because they do not treat below-ground growth. Furthermore, clipping has been shown to stimulate axillary stem production and increase overall stand longevity (Robocker, 1974; Lajeunesse, 1999). Mowing may eventually deplete root reserves over time, but this is an assumption not supported by research and results similar to clipping floral stems are possible (Lajeunesse *et al.*, 1993). Tilling of soil to cut up roots without intensive long-term cultivation is also not recommended because the root pieces are not removed and may increase stand longevity (Lajeunesse, 1999).

The waxy, hairless leaves and stems of toadflax prevent chemicals from adhering to plant foliage and absorption of chemicals. Therefore, chemical control has produced highly variable results (Lajeunesse *et al.*, 1993; Vujnovic & Wein, 1996; Lajeunesse, 1999). Dalmatian toadflax has been resistant in studies to triclopyr and fluroxypyr alone and in combination with 2,4-D amine (Ferrel & Whitson, 1989) and treatment with 2,4-D

ester has been inconsistent (Lajeunesse, 1999). Robocker (1974) achieved best control with 2,4,5-trichlorophenoxy (Silvex) applied to prostrate growth at 2.2 to 3 kg ha⁻¹ in early spring, and 3 kg ha⁻¹ in the autumn. 3,6-dichloro-2-methoxybenzoic acid (Dicamba) at 4.5 kg ha⁻¹ also provided excellent control one year after application (Lajeunesse *et al.*, 1993). 4-amino-3,5,6-trichloropicolinic acid (Granular Picloram) was more successful when applied in the fall than in the spring at the same application rate (Robocker *et al.*, 1972), with similar results found using a mixture with equal portions of picloram and fluroxypyr (Ferrel & Whitson, 1989; Hanson *et al.*, 1989). Robocker *et al.* (1961) found that 2,3,6-trichlorobenzoic acid (2,3,6-TBA) increased rates of toadflax seedling establishment, probably due to the dual control of competing downy brome at the study site. Overall, commercial chemical treatments work in the short term, but require repeated application every 3-4 years for up to 12 years (Lajeunesse *et al.*, 1993; Lajeunesse, 1999). The high cost of herbicides, their variable success, and the need for repeated treatment has typically prevented this method from being used at a large scale.

Predatory insects that are themselves not native to the U.S. have been applied as biological controls for Dalmatian toadflax. There is a great deal of controversy in the scientific community concerning the appropriateness of using non-native biocontrol agents, because of the inherent uncertainties about the insect's role in a new environment (Simberloff & Stiling, 1996). There have been cases of biocontrol success with *Lythrum salicaria* L. (purple loosestrife) (Albright *et al.* 2004) and terrible failures such as the rare *Cirsium ownbeyi* Welsh (ownbey's thistle) which was attacked by *Rhinocyllus conicus* Frölich, a seed-eating weevil introduced to control musk-thistle (Louda & O'Brien 2002). Several insect species have shown success against Dalmatian toadflax, including a defoliating moth (*Calophasia lunula* Hufnagel), an ovary-feeding beetle (*Brachypterolus pulicarius* (L.)), two seed capsule-feeding weevils (*Gymnaetron antirrhini* (Paykull)) and *Gymnaetron netum* Germar), a stem-boring weevil (*Mecinus janthinus* Germar), and a root-boring moth (*Eteobalea intermediella* (Treitschke)) (Vujnovic, 1996, De Clerck-Floate & Miller, 2002, De Clercke-Floate & Harris, 2002, Grubb *et al.* 2002). It has been reported that the two capsule-feeding weevils only attack the narrow leaved biotype of Dalmatian toadflax (broad-leaved Dalmatian toadflax is what primarily occurs in

Arizona). Intensity of attack by *M. janthinus* has increased with time in a study in Canada and shows the most promise (De Clerck-Floate & Miller, 2002).

One study suggests that *M. janthinus* in combination with *E. intermedialla* have complementary survival rates on two developmental stages of toadflax (Saner *et al.*, 1994). In Canada, *B. pulciarius* and *G. netum* attacks appear to be too rare to have a significant impact (De Clerck-Floate & Miller, 2002). Other biocontrol agents have not been established for enough time to determine their successfulness for controlling Dalmatian toadflax (Lajeunesse, 1999; De Clerck-Floate & Miller, 2002). There has been one release of *M. janthinus* and *C. lunula* in Arizona, but monitoring was not conducted and results are inconclusive (Laura Moser U.S. Forest Service, personal communication, 2004).

As a young seedling, Dalmatian toadflax is susceptible to native grass competition before the root system is established. By the end of a growing season, however, older seedlings are large enough to survive competition and successfully establish (Robocker, 1970). Grieshop and Nowierski (2002) found that toadflax seedling recruitment is more limited by interspecific competition for micro sites, than by toadflax seed availability. In a competition study, Gates and Robocker (1960) planted toadflax seeds with grass seeds on cultivated sites, and broadcast seeded onto non-cultivated sites. After 3 years the seeded grasses appeared to have no negative effect on toadflax establishment at the cultivated sites. On non-cultivated sites toadflax seedling survival was very low, likely due to competition from another exotic, cheatgrass (*Bromus tectorum*), and a native annual trefoil (*Lotus spp.*) (Gates & Robocker, 1960). Lajeunesse (1999) suggests that the best method for control with native species is to maintain or create a diverse herbaceous community where plants are actively growing and competing throughout the year. Also, the herbaceous community should represent species with shallow rooting systems to compete with toadflax seedlings, along with species with deep rooting systems to compete with juvenile and mature toadflax plants (Lajeunesse, 1999).

Policy

Most governmental levels from municipal to federal have a weed management policy (Richards *et al.*, 1998). Federal agencies are now required to restore disturbed areas using native seed when possible, as well as: 1) prevent introduction of invasive species; 2) provide for restoration of native species and habitat conditions in ecosystems that have been invaded; and 3) to develop technologies to prevent introduction of invasives and provide for environmentally sound control of invasive species (Executive Order # 13112 and Guiding Principles, February 3, 1999). States and counties also have the authority to rate weeds as “noxious” which gives these weeds a legal definition and allows for restrictions to be placed on transportation of plants and seeds, and to require treatment of weed populations (Sheley & Petroff, 1999; Sieg *et al.*, 2003). While the ability to legally control weeds is important, coordinated implementation of these policies between organizations must occur for control to be successful. Monitoring of weed populations and treatments must also be implemented consistently to track population change, assess control methods and successfully reduce exotic species populations. New regulations are also increasingly requiring the use of native species in restoration; however land managers still commonly use non-native species because of seed availability, cost, and knowledge about the species (Barro & Conard, 1987; Ken Moore, Bureau of Land Management, personal communication, 2/15/03; Dave Brewer, U.S. Forest Service, personal communication, 2/15/03).

Revegetation with Native Species: Use and History

Revegetation through seeding is one of the most common and economically efficient practices used to restore disturbed areas, and is the predominant post-fire rehabilitation method used by the U.S. Forest Service (Richards *et al.*, 1998; Robichaud *et al.*, 2000; Barro & Conard, 1987; Montalvo *et al.*, 2002). Revegetation is a common rehabilitation technique applied after disturbance events to stabilize soil, provide domestic and wildlife forage, create habitat, protect watersheds, protect property,

restore soil nutrients, prevent exotic species invasion, and for aesthetic purposes (Korb & Springer, 2003). The revegetation of disturbed areas within ponderosa pine communities of the Southwest is becoming increasingly critical as disturbance events and affects increase and the natural capabilities of an ecosystem to recover are overwhelmed. In this situation, human intervention in the form of revegetation to accelerate the recovery process may be required (Crawford *et al.*, 2001; Korb & Springer, 2003). The ultimate goal of ecological restoration through revegetation is maintaining a diverse and self-sustaining plant community that will lead to the reestablishment of ecosystem composition and function, while maintaining genetic integrity.

These long-term restoration goals are best achieved by using native plant species. Natives are advantageous because they are most likely to have adapted to local environmental conditions, some have evolved with native fauna, the natural disturbance regime, have higher production, and contain a broader genetic base that can sustain itself over a longer period (Richards *et al.*, 1998; Mortlock, 2000). Revegetation with native species after weed control can be a key factor in reducing reestablishment of exotics because native species can reduce opportunities for exotics by utilizing available resources on disturbed sites (Clary, 1988; Stohlgren *et al.*, 1999; Davis *et al.*, 2000; Grieshop & Nowierski, 2002; Cione *et al.*, 2002).

In the western U.S. the practice of revegetation began in the late 1800's for timber replacement and seeding herbaceous species for domestic forage, such as western wheatgrass (*Pascopyron smithii* (Rydb.) A. Löve) (Clary, 1989). Herbaceous revegetation to stabilize soil and protect watersheds after anthropogenic disturbances and fire stimulated experimentation with seeding methods, but generally with non-native plant species (Barro & Conard, 1987; Richards *et al.*, 1998; Robichaud *et al.*, 2000). Initially, U.S. Forest Service personnel used native species for revegetation in California by collecting seed from areas surrounding the disturbance, but found that planted seed did not emerge earlier than natural regeneration (Barro & Conard, 1987). Selected non-native species became preferred because of early emergence, high seed viability, rapid

growth, high seed production, low cost, and ease of storage and transport (Barro & Conard, 1987; Robichaud *et al.*, 2000). The earliest non-native species to be used by the Forest Service for emergency revegetation were mustards (Brassicaceae) because they were inexpensive, readily available, and could be broadcast seeded (Barro & Conard, 1987). These species were soon abandoned however because the seeds frequently washed down slope and the deep tap root system did not hold soil well. Perennial and annual ryegrass (*Lolium perenne* L. and *L. multiflorum* L.) became the exotic species of choice in the 1940's for soil stabilization because of their early emergence, mat-like growth pattern and dense, fibrous root system; they are still commonly used today (Barro & Conard, 1987).

However, several concerns have been raised about how seeded non-native species affect native species composition and abundance, leading to a number of studies focusing on ryegrass effects on native chaparral shrubs and herbaceous species (Keeley *et al.*, 1981; Richards *et al.*, 1998; Barro & Conard, 1987). One study found that ryegrass was a significant cause of native composition change, was negatively correlated with native species establishment, and reduced native shrub density (Keeley *et al.*, 1981). These effects of non-native seeded species could create a type conversion to grassland, promoting earlier seasonal fires (Barro & Conard, 1987). In a western Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forest of Montana, a study reported a possible negative impact of exotic seeded species on native grasses after 5 years (Crane *et al.*, 1983). In the pinyon-juniper (*Pinus monophylla* Torr. & Frém–*Juniperus osteosperma* (Torr.) Little) habitat of central Utah, a study found that seeded non-natives did not negatively influence native perennial grasses, but negatively affected native annual grasses (Clary, 1988).

In the southwestern ponderosa pine forests there are few studies comparing native versus exotic seeding success and the effects of exotic seeded species on the native community (Springer *et al.*, 2001). In a ponderosa pine forest within the Grand Canyon – Parashant National Monument (northwestern Arizona), a seeding experiment using only native species found that seeded plots had significantly greater richness, diversity, and

cover that unseeded plots, although seeded plots also had twice as many non-native species than unseeded plots (Springer *et al.*, 2001). Maximum species richness occurred 1.8 years after treatment and perennial native grasses dominated plant cover 2.8 years post treatment (Springer *et al.*, 2001). In a study of native seeding with soil amendments on slash pile burn scars in the ponderosa pine forest type, seeded and seeded plus soil amendment plots had greater native richness and cover and less exotic cover than unseeded, control, and amendment only plots (Korb, 2001). Total native plant cover, density and richness was greater in seeded versus unseeded plots on abandoned roads in the ponderosa forest type, though the exotic cheatgrass invaded seeded sites in the second season (Elseroad, 2001).

After the La Mesa fire in Bandelier National Monument New Mexico, species slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinnars) dropped out of the ecosystem 8 years after seeding, while the seeded species sheep fescue (*Festuca ovina* L.) increased continuously. Native graminoids also increased, though no relationship between seeded species and native species was explored (Foxy, 1994). The degree of shade, and intensity and seasonality of sunlight influences the presence, cover and density of native graminoid species (Naumburg & DeWald, 1999), and may play a significant role in the success of a revegetation project. Mutton grass (*Poa fendleriana* (Steud.) Vasey) and sedge (*Carex* spp. L.) both responded positively to midday spring/autumn sun, mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.) and screwleaf muhly (*M. virescens* Kunth (Kunth)) responded well to midday and afternoon summer sun, and squirreltail (*Elymus elymoides* (Raf.) Swezey) and prairie junegrass (*Koeleria cristata* Ledeb.) J.A. Schultes) tended to do well under a variety of light conditions and were not negatively affected by shade (Naumburg & DeWald, 1999).

Native versus Exotic Species for Revegetation

The term “native” varies between researchers, government entities, and environmental organizations and should be clearly defined prior to any revegetation project or research study. For purposes of this study, a species was considered native if it

was classified as native in Arizona according to Kearney and Peebles (1960). The term can be defined by political boundaries such as national, state, and county jurisdictions; or by ecoregion, ecosystem type, plant community, population, or genetics. Fundamentally, nativity of a species depends on the scale of the observation area (Jones, 2003). Some scientists prefer to set a distance boundary from a project site within which a species is considered locally native (e.g., 40 km) (Mortlock, 2000; Korb & Springer, 2003). In some species, as distance from a source population increases, the genetic difference increases, and genetic separation from the source population increases to a point where a species is no longer “locally native” (Lippitt *et al.*, 1994; Korb & Springer, 2003).

Locally native species are preferred for their local genetic composition versus native species purchased from a commercial grower in another state or ecosystem type. Mortlock (2000) reported that land managers in Australia found increased growth, survival and production of plants grown from local native seed versus non-local native seeds. Unfortunately, availability of local native herbaceous seed is usually limited to small quantities for purchase, is more expensive, or does not exist commercially and must be collected. Collected seeds typically have lower germination and shorter seed longevity than purchased seed because collected seeds developed under variable environmental conditions, were vulnerable to herbivory and disease, and the collected seeds may not have been thoroughly sorted like commercial seeds. Proper collection techniques are described in detail in Young and Young (1986) and Lippitt *et al.* (1994).

Using exotic species for revegetation can have detrimental effects on ecosystems including reduced germination, growth, and cover of some native species, especially fire-followers, and suppression of woody species (Barro & Conard, 1987; Cione *et al.*, 2002). Non-native species can create monocultures, convert shrublands to grasslands, reduce biodiversity, and reduce native genetic diversity and integrity through hybridization (Crane *et al.*, 1983; Barro & Conard, 1987; Clary, 1988; Schoennagel & Waller, 1999; Mortlock, 2000). Such changes in plant community composition and structure also raise concerns about cascading effects on wildlife, insects, soil nutrient composition, and hydrology (Evans *et al.*, 2001; Korb & Springer, 2003).

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CHAPTER 3

DALMATIAN TOADFLAX (*LINARIA DALMATICA* (L.) MILLER) RESPONSE TO WILDFIRE IN A SOUTHWESTERN PONDEROSA PINE FOREST

Abstract

There is little information on how fire affects the exotic, invasive species Dalmatian toadflax (*Linaria dalmatica* (L.) Miller), which has been found to alter plant communities, displace native species, reduce livestock forage, and depress land value. We measured the response of Dalmatian toadflax growth and reproduction to burn severity and the impact of toadflax on the native understory community after a 2001 wildfire that burned in a mosaic pattern of burn severity in a ponderosa pine forest of northern Arizona. We measured toadflax stem density, cover, and flowering stalks, plus richness and cover of native species in 16 burn severity X toadflax density categories for three years post-fire. Toadflax stem density, percent cover, and number of flowering stalks consistently increased in 2003, and then decreased in 2004 in all burn severity classes, although all toadflax variables remained higher in 2004 than in 2002. Toadflax stem density decreased in unburned plots but cover and flower stalks increased insignificantly. A time X burn severity interaction was significant for native plant species richness (repeated measures $p < 0.001$), but native plant species richness did not differ among toadflax density classes. Native richness increased over time, and was lowest in the high burn severity and highest in low burn severity. Native plant richness was positively correlated with native richness in the previous year (2003 $r = 0.70$, $p = 0.01$ and 2004 $r = 0.74$, $p < 0.001$). Transition matrices of plots in density classes showed that burned plots remained in the original toadflax density class or moved to a higher density class in 2004, while unburned plots shifted to a lower density class. Over three years, toadflax utilized a substantial fraction of growing resources, especially in severely burned sites. Although toadflax declined in our plots by the third year, we found evidence of its spread to previously uncolonized buffer areas around the plots. Despite the persistence of toadflax, the native plant richness appeared to be recovering in all burn severity classes.

Introduction

Wildfire size and severity have been increasing in southwestern forests in recent decades due to forest management practices and fire exclusion and wildfire suppression policies, which have led to dense overgrown forests. As a result, the fire regime, forest structure and function have changed and understory diversity has been reduced in the ponderosa pine (*Pinus ponderosa* P. & C. Lawson) forest in northern Arizona (Covington & Moore, 1994; Fulé *et al.*, 1997; Crawford *et al.*, 2001; Griffis *et al.*, 2001). Wildfires leave behind large areas of exposed mineral soils that are quickly colonized by seral opportunistic species, which can be native or exotic (Crawford *et al.*, 2001; Sieg *et al.*, 2003; Brown & Sieg, 1996). While most understory vegetation responds positively to moderate disturbance, some exotic species respond disproportionately well along a disturbance gradient and are often present after wildfires (Hobbs & Huenneke, 1992; Griffis *et al.*, 2001). Invasive exotic plant species can be detrimental to ecosystems worldwide because they can replace native vegetation, displace wildlife, out-cross with native flora, alter nutrient-cycles, hydrology, and disturbance regimes, and affect other ecosystem functions (Vitousek *et al.*, 1997; Walker & Smith, 1997). Non-native species are the second greatest cause for the listing of endangered and threatened species, with the most frequent cause being loss of habitat (Stein *et al.* 2000). Some exotic plant species have also been implicated in increasing soil erosion and controlling aspects of the biogeochemical cycle (D'Antonio & Meyerson, 2002). There is a lack of knowledge about vegetation recovery and exotic plant invasion following intense large-scale fires in southwestern ponderosa pine forests, where the likelihood of intense fires is certain (Crawford *et al.*, 2001). This study addressed the initial response and potential for persistent competition between the exotic species Dalmatian toadflax (*Linaria dalmatica* (L.) Miller) and native species.

Dalmatian toadflax was introduced to North America in 1894 as an ornamental plant from the Mediterranean region where it is native from Yugoslavia to Iran (Alex,

1962). Dalmatian toadflax has become a successful invader in many locations in the United States. It is designated as a “noxious weed” in Arizona and 11 other western states (USDA NRCS, 2004) and in 3 Canadian provinces (Rice, 2004). It is considered a serious rangeland weed in Canada and northwestern U.S. where infestations have replaced forage species for both domestic livestock and wildlife (Vujnovic & Wein, 1996; Lajeunesse, 1999). The first collection record of Dalmatian toadflax in northern Arizona was June 1940, collected by Chester Deaver on Northern Arizona University campus in Flagstaff, AZ (Deaver Herbarium, Northern Arizona University). By 2000 it was estimated that Dalmatian toadflax infested 80,000 ha. in the Coconino National Forest (Phillips & Crisp, 2001) and it is scattered throughout areas of Coconino County, with higher concentrations occurring along roads, near campsites and urban development (SWEMP Database, 2004).

Dalmatian toadflax is a short-lived perennial member of the Scrophulariaceae family, with a bright yellow flower resembling the common snapdragon. Reproduction is both asexual by rhizomes and sexual by seed, although it is self-sterile. One mature plant with ten stems was reported to produce up to 500,000 seeds which can also remain viable for ten years in the field (Robocker, 1970). An extensive root system extends up to 3 m laterally and vertically and contains large carbohydrate reserves, allowing toadflax to be competitive with native winter annuals and to sprout early in spring before natives emerge (Robocker, 1970; Lajeunesse, 1999). Throughout winter when most perennial plants are dormant, toadflax retains a green rosette which allows it to begin photosynthesis early in spring when moisture and temperature conditions are appropriate and therefore sprout earlier than many native species. Seeds are dispersed by wind and animals, although one study found 90% of common toadflax (*Linaria vulgaris*) seeds fall to the ground around the parent plant (Nadeau & King, 1991).

In the northern Arizona area toadflax growth begins in mid-March, continues until the first freeze, and flowering occurs from mid-May into October (personal observation). Similar growth and flowering patterns have been observed in Washington (Alex, 1962) (Robocker, 1970) and Montana (Lajeunesse, 1999). Dalmatian toadflax has been

credited with disrupting ecosystem composition and structure by replacing native plant species (Robocker, 1974; Lajeunesse, 1999) and even other weeds (Lange, 1958). Several toxic alkaloids are found in the leaves and stems of Dalmatian toadflax making it poisonous to wildlife and domestic livestock, but it is not known to be allelopathic (Vujnovic & Wein, 1996; Lajeunesse, 1999).

In the only other U.S. study addressing toadflax response to fire, Dalmatian toadflax biomass increased and seed production increased dramatically in an area prescribed burned, compared to an unburned area (Jacobs & Sheley, 2003). In this same study toadflax cover also increased in burned plots, was not significantly different from unburned plots. Two recent studies in Arizona reported an increase in overall exotic plant species richness and abundance after especially severe wildfires, compared with moderately burned areas and unburned sites (Crawford *et al.*, 2001; Griffis *et al.*, 2001). Griffis *et al.* (2001) also reported that abundance of native forbs increased as disturbance severity increased, but native plant species richness declined with increasing disturbance severity. Abundance and richness of native graminoids increased with moderate disturbance levels, but decreased drastically on areas severely burned by wildfire. Finally, Dalmatian toadflax invasion in northern Arizona increased after a June (before the rainy season) prescribed burn and threatened the Flagstaff pennyroyal (*Hedeoma diffusum* Greene), a plant species designated as “Sensitive” by the U.S. Forest Service (Phillips & Crisp, 2001). In this same study, Dalmatian toadflax was not present where the prescribed burn occurred after the summer rainy season, in October.

The June 2001 the Leroux wildfire burned 486 ha of ponderosa pine, quaking aspen (*Populus tremuloides* Michx.) and mixed conifer forest, on the south side of the San Francisco Peaks within the Kachina Peaks Wilderness area (Figure 1). The fire burned in a mosaic pattern, leaving patches of mixed severity across the landscape, and thus providing an opportunity for examining dalmatian toadflax response to wildfire and interaction with the native community. In this study we asked the following questions: 1) How does Dalmatian toadflax growth and reproduction respond to wildfire at variable burn severities up to three years post-fire? and 2) How does the response of Dalmatian

toadflax relate to changes in native species composition and abundance? We hypothesized that Dalmatian toadflax density, cover, and flowering stalks would increase over time in all burn severity classes, but that the rate of change will be greater in the high burn severity and high density classes. We hypothesized that toadflax density and cover would be negatively correlated with native richness and cover, so that native richness would increase over time only in plots without toadflax present. Cover and frequency of other exotic species were also anticipated to increase over time in moderate and high burn severities.

Methods

Study Area

Our study was conducted on the Leroux wildfire, located within the San Francisco Peaks - Kachina Wilderness Area of the Coconino National Forest, approximately 9.7 km north of Flagstaff in northern Arizona. Beginning on 6 June 2001 the human-ignited wildfire burned 486 ha of the San Francisco Peaks - Kachina Wilderness Area on the south-facing slope of Agassiz Peak, covering an elevation range of 2,493 m to 3,145 m. Typical of wildfires, the Leroux fire burned in a mosaic pattern, leaving a patchwork of burn severity ranging from unburned to high severity crown fire (Figure 1). Ponderosa pine was the dominant overstory species, with patches of quaking aspen, and mixed conifer communities composed of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), limber pine (*Pinus flexilis* James), and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr). Bristlecone pine (*Pinus aristata* Engelm.) occurs at higher elevations within the Leroux fire perimeter. The typical understory of this forest type is dominated by the perennial native grasses Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montanum* (Nutt.) A.S. Hitch.), muttongrass (*Poa fendleriana* (Steud.) Vasey), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), numerous annual and perennial forbs, and includes some exotic species (Korb & Springer, 2003; Fisher & Fulé, 2004). The Kachina Wilderness area has been heavily utilized throughout history, previously for logging and grazing and currently for grazing and a variety of recreation

activities. Due to these human activities exotic species, including Dalmatian toadflax, occurred in the wilderness area prior to the Leroux fire (Laura Moser U.S. Forest Service, personal communication, 2002; Fisher & Fulé, 2004).

The San Francisco Peaks were formed by volcanic activity which created a caldera that is surrounded by three main peaks, Humphreys, Agassiz, and Fremont Peaks. The Peaks are the highest points in Arizona, rising to 3851, 3766, and 3648 m, respectively. Due to its volcanic origin, soils are derived from andesite and basalt parent material and common soils are Inceptisols, Mollisols, and Alfisols (USDA Forest Service, 1995). Precipitation patterns are bimodal, characterized by periodic snow and rainfall in winter, followed by a pronounced drought in May and June, with monsoon rains occurring in July and August (Vose & White, 1991). Average annual precipitation is 53.9 cm in the Flagstaff area and the monthly mean temperature ranges from -0.8°C to 16.2°C (54-year average) (Western Regional Climate Center, 2004). Total annual precipitation from 2001-2004 was less than the long-term average: 44.7 cm (2001), 32.8 cm (2002), 45.2 cm (2003), 31.4 cm (through October 2004).

Field Methods

We assessed the response of Dalmatian toadflax to burn severity, and the response of native vegetation relative to four classes of toadflax density and to four burn severity classes on 331 permanent research plots distributed within and adjacent to the Leroux fire perimeter, at elevations ranging 2,493 to 2,804 m.

Plots were plant-centered (established around an individual plant) and chosen based on burn severity and toadflax stem density by creating sixteen burn severity X plant density categories: four burn severity categories and four toadflax stem density categories (Travis & Sutter, 1986). Burn severity was determined using a landscape burn severity map (Cocke, 2004) followed by visual confirmation according to NPS-USGS Burn Severity Mapping Project guidelines (Figure 1) (NPS - USGS,). When landscape and plot level burn severities did not agree, the plot level burn severity was used for

classification of the plot in order to more accurately describe the growing conditions affecting understory species.

Toadflax density categories were based on the number of Dalmatian toadflax stems within the plot frame: (1) none, (2) low: 1-10, (3) medium: 11-29, and (4) high: 30 +. We selected up to 28 plots per category (Table 3.1), except in the unburned severity class where only 11-16 plots were established per toadflax density class, because there were fewer individual toadflax plants present in unburned areas. A 10-m toadflax-free buffer was required for the establishment of control plots (the “no-toadflax” category). All plots were measured in the summer months of 2002, 2003, and 2004 after onset of the rainy season in mid-July when growth of many native species begins. Since plots were centered around existing plants, all data were calculated in terms of plants per plot and the total distribution of toadflax and other species in the study site could not be determined (Travis & Sutter, 1986).

Plots were 1 m² (2 m x ½ m) and permanently marked with two iron stakes at diagonal corners that were flagged. To minimize visual impact in the Wilderness Area, stakes were placed flush with the forest floor and nearby reference trees were tagged near the base facing the tagged corner stakes; tags were painted brown to conceal them. We recorded distance and direction from the reference tree to the tagged corner stakes and noted UTM coordinates, slope, plot azimuth, aspect, and elevation of each plot.

Each plant rooted in a plot was identified to species (USDA NRCS, 2004) (or genus where species was undetermined), classified as native or exotic to Arizona (Kearney & Peebles, 1960) (Table 3.2), and foliar cover was measured to the nearest 0.1%. For Dalmatian toadflax, we counted the number of stems, and number of flowering stalks, percent foliar cover. To count the actual number of flowers per plant was not feasible with our sample size and time constraints, therefore flowering stalks were counted. A flowering stalk was defined as a primary, secondary, and tertiary branching stalk off of the main system, which has multiple flowers. Additionally, we counted the number of individuals and phenologic state for other exotic plant species.

Percent cover of substrates (bare ground, rock, wood, and litter) was recorded, overstory cover (as a percentage of the plot covered), and overstory type (ponderosa pine, aspen, mixed conifer, and none: meadow) were all recorded.

Data Analysis

Plots were classified by the plot level burn severity and toadflax density class for statistical analysis. Control plots without toadflax were excluded from calculations specific only to the toadflax response. The statistical package SPSS version 12.0 was used for all analysis (SPSS for Windows, 2003). Assumptions of normality and equal variance were tested using Shapiro-Wilk's and Levene's tests, with $\alpha = 0.05$, for toadflax stem density, cover, flower stalks, and native species richness. Data met all parametric assumptions, except for a slight departure from normality for the variables stems, flower stalks, and native richness (Shapiro-Wilk $p=0.002$). However, visual inspection of the data plotted as a normal probability plot indicated that the departure was minor, so we proceeded with parametric tests (Steel & Torrie, 1980). Statistically significant differences of toadflax stem density, cover, flower stalks, and native species richness were assessed using the repeated-measures general linear model, with year as the time variable, and burn severity and density as between-subject factors.

A significant interaction between year X burn severity X density was followed by a univariate ANOVA of the change between years (Δy_1-y_2 and Δy_2-y_3), with a Bonferroni correction of $\alpha/2$. A Tukey's HSD post hoc test was used to compare individual means following a significant ANOVA. The Pearson's correlation coefficient was calculated to examine the relationship of native species richness between years, native species richness and toadflax density and cover, and native species cover and toadflax density and cover. We calculated the percentage of control plots without toadflax whose buffer zone became infested with toadflax. A transition matrix was used to summarize changes in Dalmatian toadflax density classification from 2002 to 2004 for each burn severity class. For the transition matrix, the number in each cell is the ratio of

a research plots that remained in the same density class or moved to a different density class by the third year (2004).

Results

Average Dalmatian toadflax stem density, percent cover, and flowering stalks in burned plots generally increased in 2003, then decreased slightly in 2004 in all burn severity classes, but remained greater in 2004 compared to 2002 (Table 3.3). Dalmatian toadflax stem density increased by 38 - 221% from 2002 to 2003 and decreased by 13 - 22% from 2003 to 2004 (Figure 2).

Toadflax cover increased by 65-109% from 2002 to 2003 and decreased by 2-45% from 2003 to 2004 (Figure 3). Similarly, flower stalk density increased by 16-147% from 2002 to 2003 and decreased by 11-46% from 2003 to 2004 (Figure 4). In the unburned plots, toadflax stems decreased consistently each year ($p = 0.04$), percent cover increased but not significantly each year, and flower stalks also remained similar.

There was a significant time X burn severity X density interaction for Dalmatian toadflax stem density, % cover, and flower stalks ($p < 0.001$) (Table 3.4). The change in stems from 2002 to 2003 ($\Delta y1-y2$) differed significantly among burn severity classes ($p < 0.001$) and not among density classes ($p = 0.2$); while change in stems from 2003-2004 ($\Delta y2-y3$) differed by density class ($p < 0.001$) and not burn severity ($p = 0.8$). The increase in toadflax stem density between 2002 and 2003 was greater on high burn severity plots than all other burn severity classes ($\Delta y1-y2$, Tukey's HSD $p < 0.001$), while the low and moderate severity classes, and unburned and low severity classes were similar.

For $\Delta y2-y3$ (2003 to 2004), change in stem density also differed significantly among density classes (Tukey's HSD $p < 0.049$). Average toadflax stem density declined in high density plots (-36%) and medium density plots (-28%) between 2003 and 2004,

and increased in low density plots by 24%; no-toadflax plots increased by an average of nearly 6 stems.

The $\Delta y1-y2$ for toadflax cover and flowering stalks showed a significant burn severity, density, and interaction effect ($p < 0.001$) with a separation between the high burn severity and other severity classes, as well as a separation between the no-toadflax class and other density classes (Tukey's HSD $p < 0.001$). In the high burn severity class, cover increased by 40% and flowering stalks by 69%. The $\Delta y2-y3$ of these same variables only affected among density classes ($p < 0.001$). The decrease in cover $\Delta y2-y3$ was significantly less for the low density class (Tukey's $p < 0.001$), and similar between the moderate and high density classes. The change in flowering stalk density between 2003 and 2004 differed significantly (Tukey's $p < 0.003$) among all density classes, and decreased by -58% for high density plots, -50% medium density plots, -13% for low density plots, and remained unchanged for no-toadflax plots.

Neither stem density nor percent cover of Dalmatian toadflax was significantly correlated with future toadflax stem density, or with native or exotic plant species richness. The number of flowering stalks in 2002 was positively correlated with flowering stalks in 2003 ($r = 0.66$, $p < 0.001$), and 2003 flowering stalk density was positively correlated with flower stalks in 2004 ($r = 0.52$, $p < 0.001$). The correlation of 2002 and 2004 flower stalks was weaker, $r = 0.26$, $p = 0.01$. Dalmatian toadflax stem density and cover were not correlated with substrate cover or overstory cover, and did not differ between overstory types.

Average richness of native plant species was consistently highest in low burn severity plots and lowest in the high burn severity plots over the three years (Table 3.5). Native species richness tended to increase with each year, except for the high burn severity class which did not show an increase until 2004 (Figure 5). The time X burn severity interaction was significant for native species richness ($p < 0.001$), with no significant difference among toadflax density classes ($p = 0.09$). The change in native species richness from 2002 to 2003 ($\Delta y1-y2$) and 2003 to 2004 ($\Delta y2-y3$) was

significantly different among burn severity classes ($p < 0.001$ and $p < 0.01$) (Table 3.4). The Δy_1 - y_2 in native plant species richness was similar for the following burn severity class pairs: high and moderate, moderate and low, low and unburned (Tukey's $p > 0.08$). The Δy_2 - y_3 in native richness was different between low and high burn severity (Tukey's $p < 0.007$), and all other severities were similar (Tukey's $p > 0.3$). Unexpectedly, richness of exotic plant species did not differ significantly among burn severity classes, density classes, or years, and there was no interaction effect ($p > 0.09$) (Figure 6). The most common exotic species occurring in plots, other than Dalmatian toadflax, was common mullein (*Verbascum thapsus* L.).

Native species richness was positively correlated with native plant species richness of the previous year, 2003 $r = 0.70$, $p < 0.001$ and 2004 $r = 0.74$, $p < 0.001$, although this relationship was slightly weaker across two years ($r = 0.62$, $p < 0.001$). Correlations of native species richness varied when separated into burn severity class, but richness was strongly correlated over time in every category (Table 3.6). We chose six of the most common native plant species to test for an effect of Dalmatian toadflax stem density or percent cover on native species cover. Native species chosen were bottlebrush squirrel tail (*Elymus elymoides*), Arizona fescue (*Festuca arizonica*), mountain muhly (*Muhlenbergia montana*), Wheeler's thistle (*Cirsium wheeleri* (Gray) Petrak), whip daisy (*Erigeron flagellaris* Gray), and silvery lupine (*Lupinus argenteus* Pursh). Contradicting our hypothesis, Dalmatian toadflax stem density and percent cover were not significantly correlated ($p > 0.05$) with cover of any one of these six native species.

None of the Dalmatian toadflax control plots (no-toadflax) were invaded by toadflax in 2003, and only two plots were invaded in 2004. However, the 10-m toadflax-free buffer zone was invaded by toadflax in 31.5% (24) plots in 2004. Of these plots, 58% were categorized as high burn severity, 17% were moderate severity, 21% were low severity, and 4% were unburned. Dalmatian toadflax disappeared from six plots in 2004 where toadflax was present in the previous two years; three of these plots were unburned and one plot was in each burn severity class.

Transition matrices of plots in density classes showed that burned plots either remain in their original toadflax density class or moved to a higher density class in 2004 (Table 3.7a, b, c, d). The percent of plots moving into or remaining in the high density class decreased with decreasing burn severity. In the unburned class, more low density plots shifted to a greater density class (47%), while 39% of medium density plots shifted to lower density classes and half remained as medium. Fewer of the unburned-high density plots remained as high density in 2004 (36%) than in any other burn severity category. Since only two plots became invaded over the three years the “none” density class remained similar in the matrices.

Discussion

We did not expect toadflax plants to reach a critical maximum density by the second year, and therefore it was unexpected to find a decrease in Dalmatian toadflax growth and reproduction in the third year. One possible explanation is that fire effects such as a nutrient pulse, litter removal, removal of competing plants, and increased soil temperature can be short-lived, and it is possible that the rapid growth of toadflax and subsequent decline was a reflection of these transient effects (DeBano *et al.*, 1998). Toadflax may have increased to a level higher than experienced under unburned conditions, consumed limiting resources, reached a critical threshold, and declined to a more sustainable level for the species. Results of repeated measures tests support this concept because burn severity was the driving factor for toadflax stem density, cover, and flower stalk increases between 2002 and 2003, but was not a significant factor in 2004. A similar increase in toadflax biomass one year post fire was described by Jacobs and Sheeley (2003) and was attributed to a nutrient pulse after fire. Similar responses in native species are also attributed to a nutrient release by fire (Phillips & Crisp, 2001; Vose & White, 1991).

Secondly, we qualitatively discovered that a decline in toadflax density and cover within the plots in 2004 did not necessarily reflect a decline in toadflax infestation

surrounding the plot, and that toadflax actually migrated out of the plots (Figure 7). Repeated measures tests also showed that toadflax stem density was the significant factor driving the change of toadflax stems, cover and flower stalks in 2004, supporting the idea that Dalmatian toadflax reached a maximum critical threshold which forced it to spread outside the plot to access resources. This could also explain why toadflax disappeared from six previously infested plots in 2004 and was present immediately outside the plot frame. Since our experimental design focused on the response of an individual plant, we could not quantify an increase in patch size or actual spread across the landscape. This pattern of toadflax spread outside of the plot was observed repeatedly by field crews and is documented visually through chronologic photographs (Figure 7). Using plant centered plots was beneficial because we were able to accurately quantify the response of individual toadflax plants to fire severity. However, future studies could employ a nested plot design to capture both individual plant and patch level responses (Pauchard *et al.*, 2003). Pauchard *et al.* (2003) conducted a multi-scale study on invasion pattern of common toadflax (*L. vulgaris*) that revealed that dense patches tended to disperse rather than aggregate, and younger stands tended to be clumped while older stands were dispersed, similar to the spread observed in our study.

Dalmatian toadflax growth and reproduction were strongly related to burn severity and were greatest in high burn severity areas. While toadflax response variables increased in all burned plots, there was disproportionately positive toadflax population response in conjunction with a disproportionately negative response of native plant species richness in the high severity burn. These results were similar to other studies in northern Arizona that documented increases of other exotic species on high severity burns (Crawford *et al.*, 2001; Griffis *et al.*, 2001). Should the increase in the number and size of large stand-replacing fires observed in recent years in the southwestern U.S. (Swetnam & Baisan, 1996) continue in the future, large patches of moderate and high severity burn will be available for colonization and spread of Dalmatian toadflax. Even though initial fire effects can be short-lived, it gives Dalmatian toadflax a long-term competitive advantage that is maintained in following years by higher density established after the fire.

In addition to wildfires, as forest restoration treatments involving tree thinning and prescribed fire are increasingly proposed and implemented we need to consider the effects on Dalmatian toadflax. Even at lower fire severities typical of prescribed fires, toadflax is capable of establishing and increasing significantly, and becoming a serious obstacle for restoration practitioners to overcome. To successfully manage this invasive exotic plant species while attempting to reduce fuels and thin forests, it will be imperative to plan control and monitoring methods before treatments are implemented. Conducting weed control (pulling, chemical, or clipping) before initiating prescribed fire could reduce amount of stored resources available for resprouting and prevent seed dispersal by crews. Additional post-fire control should be conducted for several years to remove seedlings that are stimulated by the disturbance and resprouting adults. Other studies have found that Dalmatian toadflax seedlings are susceptible to competition before roots become established, and establishment of cool season native plants may provide sufficient competition to prevent toadflax seedling survival (Lajeunesse 1999). An annual or biennial (spring and fall) monitoring plan should be implemented to monitor the effectiveness of weed control treatments and toadflax population response.

Native species richness responded well to low and moderate burn severity as expected, but unexpectedly native richness was not significantly correlated with Dalmatian toadflax density. In general, understory species in northern Arizona are adapted to a low severity fire regime, which enhances growth, and many species rely on fire to reproduce (Vose & White, 1991; Griffis *et al.*, 2001; Korb & Springer, 2003). The fact that native plant species richness was greater in low burn severity plots than unburned plots, and lowest in high severity plots is consistent with the intermediate disturbance hypothesis (Connell, 1978) and underscores the important role of fire in maintaining ecosystem composition and function in ecosystems where fire is a primary disturbance mechanism. The benefits associated with fire to native plants may have outweighed any negative effects of toadflax on native richness and cover, explaining the lack of relationship in our study.

However, the small plot size used in the study may also have contributed to the lack of a significant correlation between toadflax population parameters and native plant species richness and cover. With plant-centered plots that were established around a discrete individual not associated with a larger patch, we could only measure the effect of that one toadflax plant on native species immediately adjacent to the plant, and could not measure how a larger patch may affect the native community. This issue of scale is one possible explanation for our results, which contradicted other studies that linked increase in exotic species abundance and richness with declines in native plant species richness and cover (Elton, 1958; Robocker, 1974; Vitousek *et al.*, 1997; D'Antonio & Meyerson, 2002). At a clonal patch scale, *L. vulgaris* (common toadflax) native plant cover was significantly lower in patch centers where *L. vulgaris* ramet density and height was the greatest when compared to the patch edge (Pauchard *et al.*, 2003). Since we measured plant cover by species which is not additive due to overlapping plants, we could not analyze the effect of toadflax on total native plant cover. A second possible explanation for the lack of correlation between native richness and cover and toadflax density and cover could be that the positive effects of the fire on native species outweighed the negative effects of toadflax presence. Continuing this study for several more years, after most fire effects have dissipated, may capture a change in native species presence related to toadflax presence.

Contrary to our hypothesis, exotic species richness did not change significantly over time, and was not significantly correlated with burn severity. Though not significantly different between burn severity classes, there was a trend of increasing exotic species richness with increasing burn severity. This trend of higher exotic richness with increasing burn severity is consistent with other studies in northern Arizona that noted that exotic species were likely to occur on severely burned sites (Griffis *et al.*, 2001; Crawford *et al.*, 2001; Korb, 2001). Again, the issue of scale is important and it is possible that our plot size was too small to adequately detect a relationship between burn severity and exotic richness. It is also possible that the duration of this study was not sufficient to capture the change in exotic richness that could occur over a longer period of time.

The increasing then decreasing growth rates of toadflax over time under burned conditions resulted in there being no predictability over time of toadflax stem density or cover. Furthermore, the decline in toadflax on infested plots in 2004 may be contradicted by the apparent spread over the landscape. However, we were able to calculate transition matrices based on density classification in 2002 and 2004. This method was similar to that used in a study examining the transitional stages of grassland converting to woodland (Scanlan & Archer, 1991). In the burned categories, plots consistently moved from lower toadflax density classes to higher density classes. The percent of plots moving into or remaining in the high density class increased with increasing burn severity, indicating consistent response of toadflax to fire. From these results a manager can expect a toadflax plant to increase to a high density category plant regardless of the initial number of stems, even if the burn severity is low.

The strong relationship between fire severity and toadflax growth needs to be addressed by land managers both after wildfires and before prescribed burning, by controlling existing Dalmatian toadflax populations, monitoring the effectiveness of control efforts, and preventing new populations from becoming established. Our results indicate that fire benefits Dalmatian toadflax more in the first two years after fire, and control efforts should be focused on high and moderate burn severity areas. Although toadflax increases were highest on high burn severity plots, toadflax stem densities also increased over the three years on low severity burn plots; thus even low severity fires may encourage toadflax.

In the absence of fire or when fire effects become an insignificant factor, prioritizing toadflax control could be based on stem density. Low density plots increased in density over time, while high and moderate density classes decreased, indicating that control efforts should be focused on lower density classes. Since toadflax density appears to be self-regulating by spreading outward after attaining a critical threshold, the treatment of lower density areas along the periphery of a toadflax patch or satellite individuals may be effective at reducing spread. It would be beneficial for future

research to explore the effectiveness of different treatment methods, timing of treatment on toadflax production, and timing of treatment on carbohydrate root reserves. A multi-scale study incorporating patch size and distribution across the landscape could adequately describe the dynamics of Dalmatian toadflax spread and affects on the native understory community.

Table 3.1. Total number of plots in each burn severity by Dalmatian toadflax stem density class in 2002.

Toadflax Stem Density Class	Burn Severity Class¹				Total
	Unburned	Low	Moderate	High	
None	16	22	21	20	79
Low (1-10)	17	21	23	28	89
Medium (11-29)	13	27	22	22	84
High (30+)	11	19	26	23	79
Total	57	89	92	93	331

¹ Based on Cocke (2004) and NPS-USGS (2002).

Table 3.2. List of plant species, by family, found in study plots during all three years, and information on nativity and life history strategy. USDA NRCS (2004) is the authority for scientific nomenclature. Kearney and Peebles (1960) is the authority for Arizona nativity.

Family	Genus	Species	Common Name	Nativity ¹	Life History Strategy ²
Apiaceae					
	<i>Pseudocymopterus</i>	<i>montanus</i>	alpine false springparsley	N	P
Asteraceae					
	<i>Achillea</i>	<i>millefolium</i> L.	common yarrow	N	P
	<i>Agoseris</i>	<i>glauc</i> (Pursh) Raf.	pale agoseris	N	P
	<i>Ambrosia</i>	<i>psilostachya</i> DC.	Cuman ragweed	I	P
			smallleaf		
	<i>Antennaria</i>	<i>parvifolia</i> Nutt.	pussytoes	N	P
		<i>carruthii</i> Wood ex	Carruth's		
	<i>Artemisia</i>	Carruth.	sagewort	N	P
	<i>Artemisia</i>	<i>ludoviciana</i> Nutt.	white sagebrush	N	P
		<i>dissecta</i> (Gray)			
	<i>Bahia</i>	Britt.	ragleaf bahia	N	B
	<i>Cirsium</i>	<i>sp.</i> P.Mill.	thistle	U	U
	<i>Cirsium</i>	<i>vulgare</i> (Savi) Ten.	bull thistle	I	B
		<i>wheeleri</i> (Gray)			
	<i>Cirsium</i>	Petrak	Wheeler's thistle	N	P
		<i>divergens</i> Torr. &	spreading		
	<i>Erigeron</i>	Gray	fleabane	N	B
	<i>Erigeron</i>	<i>flagellaris</i> Gray	trailing fleabane	N	B
		<i>formosissimus</i>			
	<i>Erigeron</i>	Greene	beautiful fleabane	N	P
	<i>Erigeron</i>	<i>sp.</i> L.	fleabane	U	P
		<i>speciosus</i> (Lindl.)			
	<i>Erigeron</i>	DC.	aspen fleabane	N	P
	<i>Heliomeris</i>	<i>multiflora</i> Nutt.	showy goldeneye	N	P
		<i>fendleri</i> Schultz-	yellow		
	<i>Hieracium</i>	Bip.	hawkweed	N	P
	<i>Lactuca</i>	<i>serriola</i> L.	prickly lettuce	I	P
		<i>schiedeana</i> (Less.)	pineland		
	<i>Laennecia</i>	Nesom	marshtail	N	A
		<i>multilobata</i> (Torr.			
		& Gray ex Gray)			
		W.A. Weber & A.	lobeleaf		
	<i>Packera</i>	Löve	groundsel	N	P
		<i>macounii</i> (Greene)			
	<i>Pseudognaphalium</i>	Kartesz, comb. nov.	clammy cudweed	N	AB

<i>Pseudognaphalium</i>	ined. <i>sp. Kirp eremophilus</i>	cudweed	U	AB
<i>Senecio</i>	Richards	desert ragwort thread-leaf	N	P
<i>Senecio</i>	<i>flaccidus</i> Less.	ragwort	N	P
<i>Solidago</i>	<i>sp. L.</i>	goldenrod threenerve	N	P
<i>Solidago</i>	<i>velutina</i> DC.	goldenrod	N	P
<i>Stephanomeria</i>	<i>sp. Nutt.</i>	wirelettuce	U	ABP
	<i>officinale</i> G.H.	common		
<i>Taraxacum</i>	Weber ex Wiggers	dandelion	I	P
<i>Tragopogon</i>	<i>dubius</i> Scop.	yellow salsify	I	AB
Berberidaceae				
<i>Mahonia</i>	<i>repens</i> (Lindl.) G. Don	Oregon-grape	N	P
Boraginaceae				
<i>Lappula</i>	<i>occidentalis</i> (S. Wats.) Greene	flatspine stickseed	N	AB
<i>Lithospermum</i>	<i>multiflorum</i> Torr. Ex Gray	manyflowered gromwell	N	P
<i>Mertensia</i>	<i>franciscana</i> Heller	Franciscan bluebells	N	P
Brassicaceae				
<i>Arabis</i>	<i>fendleri</i> (S. Wats.) Greene	Fendler's rockcress	N	P
<i>Arabis</i>	<i>sp. L.</i>	rockcress	U	U
<i>Arabis or Pennellia</i>	<i>sp. L. Nieuwl.</i>		U	U
<i>Pennellia</i>	<i>longifolia</i> (Benth.) Rollins	longleaf mock thelypody	N	B
<i>Pennellia</i>	<i>sp. Nieuwl.</i>	unknown Pennelia	N	BP
Caryophyllaceae				
<i>Arenaria</i>	<i>lanuginose</i> (Michx.) Rohrb	spreading sandwort	N	P
<i>Silene</i>	<i>scouleri</i> Hook.	Scouler's campion	N	P
Chenopodiaceae				
<i>Chenopodium</i>	<i>fremontii</i> Gray	Fremont's goosefoot	N	A
<i>Chenopodium</i>	<i>graveolens</i> Willd. <i>leptophyllum</i>	fetid goosefoot narrowleaf	N	A
<i>Chenopodium</i>	(Moq.) Nutt. ex S.	goosefoot	N	A
<i>Chenopodium</i>	<i>sp. L</i>	goosefoot	U	A

Cyperaceae

	<i>geophila</i>	White Mountain		
<i>Carex</i>	Mackenzie	Sedge	N	P
<i>Carex</i>	<i>rossii</i> Boott	Ross' sedge	N	P
<i>Carex</i>	<i>siccata</i> Dewey	dry-spike sedge	N	P
<i>Carex</i>	<i>sp. L.</i>	upland sedge	N	P

Dennstaedtiaceae

	<i>aquilinum</i> (L.)	western		
<i>Pteridium</i>	Kuhn	brackenfern	N	P

Euphorbiaceae

<i>Euphorbia</i>	<i>sp. L.</i>	spurge	U	AP
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Fabaceae

		groundcover		
<i>Astragalus</i>	<i>humistratus</i> Gray	milkvetch	N	P
		Rusby's		
<i>Astragalus</i>	<i>rusbyi</i> Greene	milkvetch	N	P
<i>Astragalus</i>	<i>sp. L.</i>	milkvetch	N	P
	<i>lanszwertii</i> Kellogg			
<i>Lathyrus</i>	var. <i>leucanthus</i>	Nevada pea	N	P
<i>Lathyrus/Vicia</i>	<i>sp. L/L.</i>	vetch or peavine	U	AP
<i>Lotus</i>	<i>sp. L.</i>	birdsfoot trefoil	N	P
	<i>wrightii</i> (Gray)	Wright's		
<i>Lotus</i>	Greene	deervetch	N	P
<i>Lupinus</i>	<i>argenteus</i> Pursh	silver lupine	N	P
<i>Lupinus</i>	<i>hillii</i> Greene	Hill's lupine	N	P
		Lambert's		
<i>Oxytropis</i>	<i>lambertii</i> Pursh	locoweed	N	P
		Mountain		
<i>Thermopsis</i>	<i>montana</i> Nutt.	Goldenbanner	N	P
	<i>gymnocarpon</i> Nutt.			
<i>Trifolium</i>	ssp. <i>gymnocarpon</i>	hollyleaf clover	N	P
<i>Trifolium</i>	<i>repens</i> L.	white clover	I	P
<i>Trifolium</i>	<i>sp. L.</i>	clover	U	P
	<i>americana</i> Muhl.			
<i>Vicia</i>	ex Willd.	American vetch	N	P
<i>Vicia</i>	<i>sp. L.</i>	vetch	N	P

Gentianaceae

	<i>speciosa</i> Dougl. ex			
<i>Frasera</i>	Griseb.	showy frasera	N	P

Geraniaceae

	<i>cicutarium</i> (L.)	redstem stork's		
<i>Erodium</i>	L'Hér. ex Ait.	bill	I	A
		pineywoods		
<i>Geranium</i>	<i>caespitosum</i> James	geranium	N	P
<i>Geranium</i>	<i>sp. L.</i>	geranium	N	P

Hydrophyllaceae

<i>Nama</i>	<i>dichotomum</i> Ruiz & Pavón) Choisy	wishbone fiddleleaf	N	A
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Iridaceae

<i>Iris</i>	<i>missouriensis</i> Nutt.	Rocky Mountain iris	N	P
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Lamiaceae

<i>Marrubium</i>	<i>vulgare</i> L.	horehound	I	P
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Nyctaginaceae

<i>Mirabilis</i>	<i>decipiens</i> (Standl.) Standl.	broadleaf four o'clock	N	P
<i>Mirabilis</i>	<i>sp.</i> L.	four o'clock	N	P

Onagraceae

<i>Epilobium</i>	<i>brachycarpum</i> K. Presl	tall annual willowherb	N	A
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Pinaceae

<i>Pinus</i>	<i>ponderosa</i> P.& C. Lawson	ponderosa pine	N	P
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Poaceae

<i>Agropyron</i>	<i>sp.</i> Gaertn.	wheatgrass	U	P
<i>Blepharoneuron</i>	<i>tricholepis</i> (Torr.) Nash	pine-dropseed	N	P
<i>Bromus</i>	<i>anomalus</i> Rupr. ex Fourn.	nodding brome	N	P
<i>Bromus</i>	<i>ciliatus</i> L.	fringed brome	N	P
<i>Bromus</i>	<i>sp.</i> L.	brome	U	AP
<i>Bromus</i>	<i>tectorum</i> L.	cheatgrass	I	A
<i>Elymus</i>	<i>elymoides</i> (Raf.) Swezey	western bottle- brush grass	N	P
<i>Festuca</i>	<i>arizonica</i> Vasey	Arizona fescue	N	P
<i>Hordeum</i>	<i>jubatum</i> L.	foxtail barley	N	P
<i>Koeleria</i>	<i>macrantha</i> (Ledeb.) J.A. Schultes	prairie junegrass	N	P
<i>Leymus</i>	<i>cinereus</i> (Scribn. & Merr.) A. Löve	basin wildrye	N	P
<i>Muhlenbergia</i>	<i>montana</i> (Nutt.) A.S. Hitchc.	mountain muhly	N	P
<i>Muhlenbergia</i>	<i>rigens</i> (Benth.) A.S. Hitchc.	deergrass	N	P
<i>Muhlenbergia</i>	<i>sp.</i> Schreb.	muhly	U	U
<i>Muhlenbergia</i>	<i>virescens</i> (Kunth) Kunth	screwleaf muhly	N	P
<i>Muhlenbergia</i>	<i>wrightii</i> Vasey ex Coul.	spike muhly	N	P

<i>Pascopyrum</i>	<i>smithii</i> (Rydb.) A. Löve	western wheatgrass	N	P
<i>Piptochaetium</i>	<i>pringlei</i> (Beal) Parodi	Pringle's spear grass	N	P
<i>Poa</i>	<i>fendleriana</i> (Steud.) Vasey	muttongrass	N	P
<i>Poa</i>	<i>pratensis</i> L.	Kentucky bluegrass	I	P
<i>Poa</i>	<i>sp.</i> L.	bluegrass	U	P
	<i>ponticum</i> (Podp.) Z.-W. Liu & R.-C. Wang			
<i>Thinopyrum</i>		tall wheatgrass	I	P
Polemoniaceae				
<i>Phlox</i>	<i>gracilis</i> (Hook.) Greene	slender phlox	N	A
Polygonaceae				
<i>Polygonum</i>	<i>douglasii</i> Greene	Douglas' knotweed	N	A
<i>Polygonum</i>	<i>sp.</i> L.	knotweed	U	AP
Ranunculaceae				
<i>Thalictrum</i>	<i>fendleri</i> Engelm. ex Gray	Fendler's meadowrue	N	P
Rhamnaceae				
<i>Ceanothus</i>	<i>fendleri</i> Gray	Fendler's ceanothus	N	P
Rosaceae				
<i>Potentilla</i>	<i>crinita</i> Gray	bearded cinquefoil	N	P
<i>Potentilla</i>	<i>hippiana</i> Lehm.	woolly cinquefoil	N	P
<i>Potentilla</i>	<i>sp.</i> L.	cinquefoil	N	P
<i>Potentilla</i>	<i>subviscosa</i> Greene	Navajo cinquefoil	N	P
<i>Rosa</i>	<i>woodsii</i> Lindl.	Woods' rose	N	P
Rubiaceae				
<i>Houstonia</i>	<i>wrightii</i> Gray	pygmy bluet	N	P
Salicaceae				
<i>Populus</i>	<i>tremuloides</i> Michx.	quaking aspen	N	P
Scrophulariaceae				
<i>Castilleja</i>	<i>integra</i> Gray	wholeleaf Indian paintbrush	N	P
<i>Castilleja</i>	<i>sp.</i> Mutis ex L. f. <i>dalmatica</i> (L.) P. Mill.	Indian paintbrush	N	P
<i>Linaria</i>		Dalmatian toadflax	I	P
	<i>barbatus</i> (Cav.) Roth	beardlip		
<i>Penstemon</i>		penstemon	N	P

<i>Penstemon</i>	<i>linarioides</i> Gray	toadflax penstemon unknown	N	P
<i>Penstemon</i>	<i>sp.</i> Schmidel	penstemon upright blue	N	P
<i>Penstemon</i>	<i>virgatus</i> Gray	beardtongue	N	P
<i>Verbascum</i>	<i>thapsus</i> L.	common mullein	I	B
Solanaceae				
<i>Nicotiana</i>	<i>attenuate</i> Torr. ex S. Wats.	coyote tobacco	N	A
Verbenaceae				
<i>Verbena</i>	<i>macdougalli</i> Heller	New Mexico vervain	N	P

¹ N = native, I = introduced, U = unknown

² P = perennial, A = annual, B = biennial

Table 3.3. Means (S. E.) for Dalmatian toadflax stem density, percent cover, and flowering stalk density by burn severity and toadflax density class for three years post-fire.

Burn severity Density class	Toadflax Stems (no./m ²)			Toadflax Cover (%)			Toadflax Flowering Stalks (no./m ²)		
	2002	2003	2004	2002	2003	2004	2002	2003	2004
Unburned									
No toadflax	0	0	0	0	0	0	0	0	0
Low density	6 (0.5)	16 (3.2)	13 (3.3)	1.6 (0.2)	2.8 (0.5)	7 (2.5)	25 (7.1)	53 (15.1)	82 (25.1)
Medium density	18 (1.2)	17 (3.8)	13 (2.2)	3.2 (1)	4.1 (1)	4 (1.1)	70 (27.8)	62 (20.3)	59 (20.7)
High density	65 (9.9)	32 (6.4)	21 (5.2)	9.4 (2.8)	11 (5)	8 (3.9)	296 (98)	331 (95.6)	194 (110.5)
Low Severity									
No toadflax	0	0	0	0	0	0	0	0	0
Low density	6 (0.7)	33 (6.6)	15.6 (2.7)	2.5 (0.5)	5.9 (0.7)	5 (0.9)	25 (5)	80 (22.2)	62 (17.2)
Medium density	17.6 (91.3)	51 (13.0)	20 (2.7)	5.7 (0.8)	14.2 (2.2)	6 (1.3)	82 (14.2)	202 (25.6)	76 (23.8)
High density	45 (2.4)	46 (8.4)	39 (5.8)	15.1 (2.8)	19.9 (4.2)	12 (2.6)	82 (14.2)	295 (55.3)	186 (43.6)
Moderate Severity									
No toadflax	0	0	0	0	0	0	0	0	0
Low density	6 (0.7)	21 (3.7)	22 (3.9)	2.6 (0.5)	6.2 (1)	9 (2.9)	39 (97.9)	90 (15.7)	100 (27.4)
Medium density	20 (1.5)	47 (7.5)	36 (5.2)	5.5 (0.7)	17.7 (3.8)	12 (2.7)	83 (13.1)	225 (33.5)	132 (21.5)
High density	47 (3.7)	61 (10.3)	49 (7.9)	17.3 (3.7)	29.7 (5.4)	21 (5.3)	257 (44)	510 (113)	230 (53.8)
High Severity									

No toadflax	0	0	3 (0)	0	0	0.25 (0)	0	0	0
Low density	6 (0.5)	67 (8.9)	84 (13.60)	4.5 (4.2)	36.9 (4.2)	44 (5.8)	61 (10.7)	491 (69.7)	524 (102)
Medium density	19 (1.2)	64 (16.2)	60 (11.1)	18.2 (4.6)	35.5 (5.6)	22 (4.8)	250 (43.4)	485 (92)	259 (50)
High density	59 (5.6)	71 (14.2)	67 (9.7)	27.5 (4.7)	42 (4.9)	23 (4.5)	413 (53.8)	729 (107)	345 (65.4)

Table 3.4. Summary of statistical tests of significance for Dalmatian toadflax stems, cover, and flowering stalks. Repeated measures was used to test for the year x burn severity x density interaction, followed by an ANOVA on the difference between years.

Response Variable	P value	Response Variable	P value
Toadflax Stems (no./m²)		Native Species Richness	
Year x Burn Severity x Density	p < 0.001	Year x Burn Severity	p < 0.001
Δy1-y2		Δy1-y2	
Burn severity	p < 0.001	Burn severity	p < 0.001
Density	p = 0.2	Δy2-y3	
Δy2-y3		Burn severity	p < 0.001
Burn severity	p = 0.8		
Density	p < 0.001		
Toadflax Cover (%)			
Year x Burn Severity x Density	p < 0.001		
Δy1-y2			
Burn severity	p < 0.001		
Density	p < 0.001		
Severity x Density	p < 0.001		
Δy2-y3			
Burn severity	p = 0.5		
Density	p < 0.001		
Toadflax Flower stalks (no./m²)			
Year x Burn Severity x Density	p < 0.001		
Δy1-y2			
Burn severity	p < 0.001		
Density	p < 0.001		
Severity x Density	p = 0.001		
Δy2-y3			
Burn severity	p = 0.1		
Density	p < 0.001		

Table 3.5. Average (S. E.) native and exotic plant species richness by burn severity and toadflax density class for three years post-fire.

Burn severity Density class	Native Plant Species Richness			Exotic Plant Species Richness		
	2002	2003	2004	2002	2003	2004
Unburned						
No toadflax	4.6 (0.4)	6.6 (1.8)	6.9 (0.6)	0	0.1 (0.1)	0.1 (0.07)
Low density	4.5 (0.6)	6.2 (0.7)	6.1 (0.6)	1 (0)	1.1 (0.1)	1.1 (0.1)
Medium density	4.7 (0.6)	6.2 (0.6)	7.2 (0.7)	1.2 (0.1)	1.1 (0.1)	1.2 (0.2)
High density	5.3 (0.8)	6.4 (0.6)	6.4 (0.7)	1.2 (0.1)	1.2 (0.1)	1.1 (0.7)
Low Severity						
No toadflax	4.4 (0.4)	5.9 (0.6)	6.5 (0.4)	0.1 (0.1)	1.2 (0.1)	1.3 (0.1)
Low density	5.6 (0.5)	6.8 (0.5)	7.1 (0.4)	1.4 (0.1)	1.3 (0.1)	1.3 (0.1)
Medium density	6.3 (0.4)	8 (0.50)	7.3 (0.5)	1.4 (0.1)	1.3 (0.1)	1.3 (0.1)
High density	6.1 (0.5)	7.4 (2.7)	6.8 (0.4)	1.2 (0.1)	1.2 (0.1)	1.2 (0.1)
Moderate Severity						
No toadflax	4.1 (0.4)	4.6 (0.4)	4.9 (0.5)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)
Low density	5.8 (0.4)	6.4 (0.4)	6.9 (0.4)	1.3 (0.1)	1.2 (0.1)	1.3 (0.1)
Medium density	6.4 (0.5)	6.7 (0.5)	7.2 (0.6)	1.2 (0.1)	1.2 (0.1)	1.2 (0.1)
High density	5.9 (0.4)	7 (0.5)	6.5 (0.4)	1.3 (0.1)	1.2 (0.1)	1.3 (0.1)
High Severity						
No toadflax	4 (0.5)	4.3 (2.6)	5.4 (0.5)	0.4 (0.1)	0.5 (0.1)	0.7 (0.2)
Low density	2.9 (0.4)	3.5 (0.4)	4.3 (0.4)	1.4 (0.1)	1.6 (0.1)	1.5 (0.1)
Medium density	6.1 (0.7)	5.3 (0.5)	6.4 (0.5)	1.4 (0.1)	1.4 (0.1)	1.2 (0.1)
High density	5.9 (2.3)	5 (0.5)	5.3 (0.4)	1.4 (0.1)	1.3 (0.1)	1.2 (0.1)

Table 3.6. Pearson's correlation coefficient (r) of native species richness between years and by burn severity class.

Burn Severity	year1-year2	year2-year3	year1-year3
Unburned	0.68 (p<0.001)	0.68 (p<0.001)	0.53 (p<0.001)
Low severity	0.66 (p<0.001)	0.75 (p<0.001)	0.58 (p<0.001)
Moderate severity	0.65 (p<0.001)	0.71 (p<0.001)	0.69 (p<0.001)
High severity	0.81 (p<0.001)	0.70 (p<0.001)	0.63 (p<0.001)

Table 3.7. Transition matrices of the probability (proportion) of plots changing toadflax stem density class from 2002 to 2004, by burn severity class: a) unburned, b) low burn severity, c) moderate burn severity, and d) high burn severity. A value equals the ratio of plots that remained in or moved density classes from 2002 to 2004

a) Unburned

Density in year 3	Density class in year 1			
	None	Low	Medium	High
None	1.0	0.06	0.08	0.09
Low (1-10)	0	0.47	0.31	0.36
Medium (11-29)	0	0.47	0.54	0.18
High (30+)	0	0	0.08	0.36
Total Plots	15	17	13	11

b) Low burn severity

Density in year 3	Density class in year 1			
	None	Low	Medium	High
None	1.0	0	0	0.05
Low (1-10)	0	0.57	0.22	0.05
Medium (11-29)	0	0.33	0.48	0.32
High (30+)	0	0.1	0.3	0.58
Total Plots	19	21	27	19

c) Moderate burn severity

Density in Year 3	Density class in year 1			
	None	Low	Medium	High
None	0.95	0	0.05	0
Low (1-10)	0	0.39	0.09	0
Medium (11-29)	0.05	0.39	0.50	0.27
High(30+)	0	0.22	0.36	0.73
Total Plots	21	23	22	26

d) High burn severity

Density in Year 3	Density class in year 1			
	None	Low	Medium	High
None	0.95	0	0.05	0
Low (1-10)	0.05	0.11	0.09	0.13
Medium (11-29)	0	0.14	0.23	0.13
High (30+)	0	0.75	0.64	0.74
Total Plots=	20	28	22	23

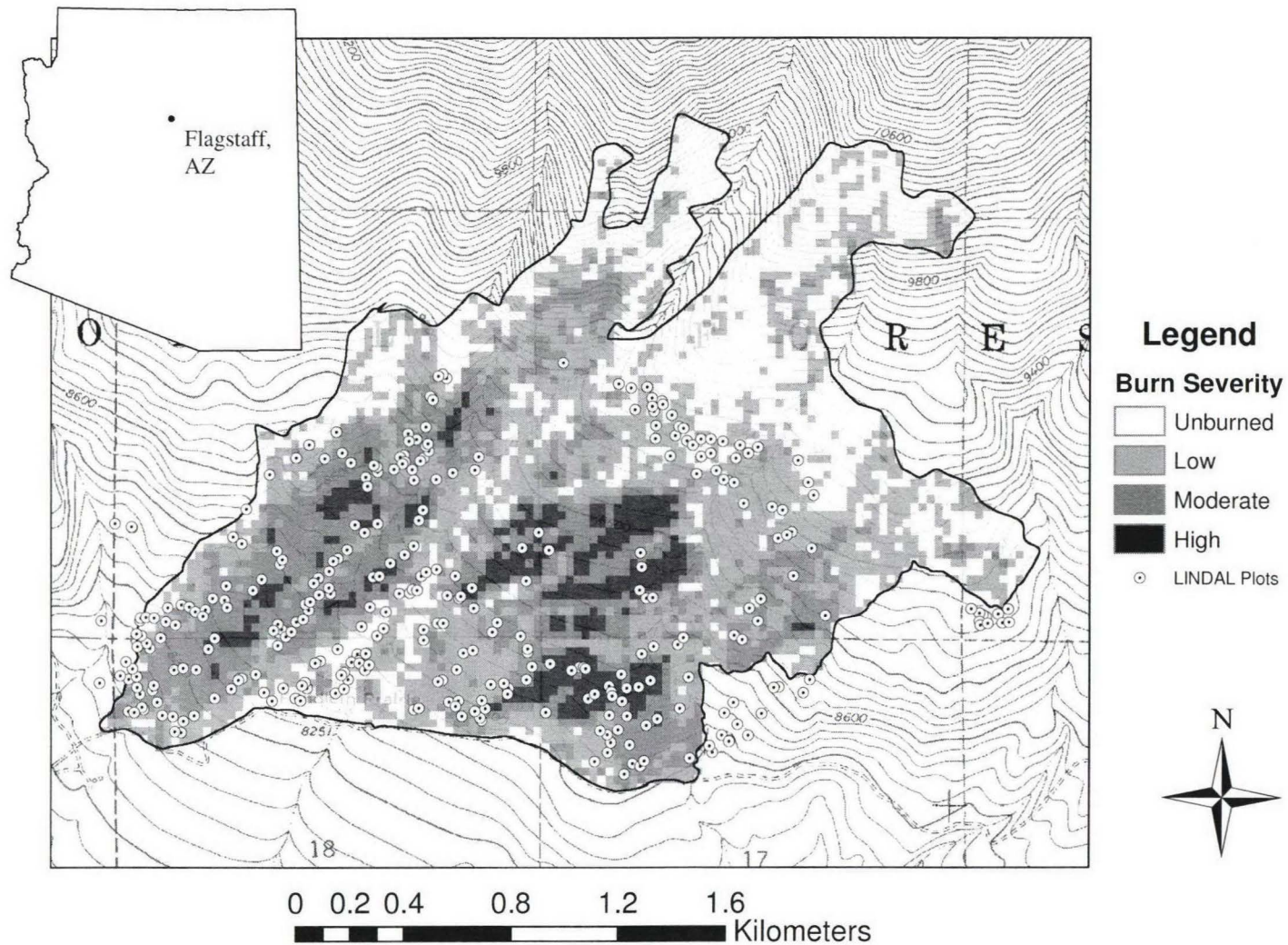


Figure 1. Leroux fire burn severity map with Dalmatian toadflax monitoring plot locations.

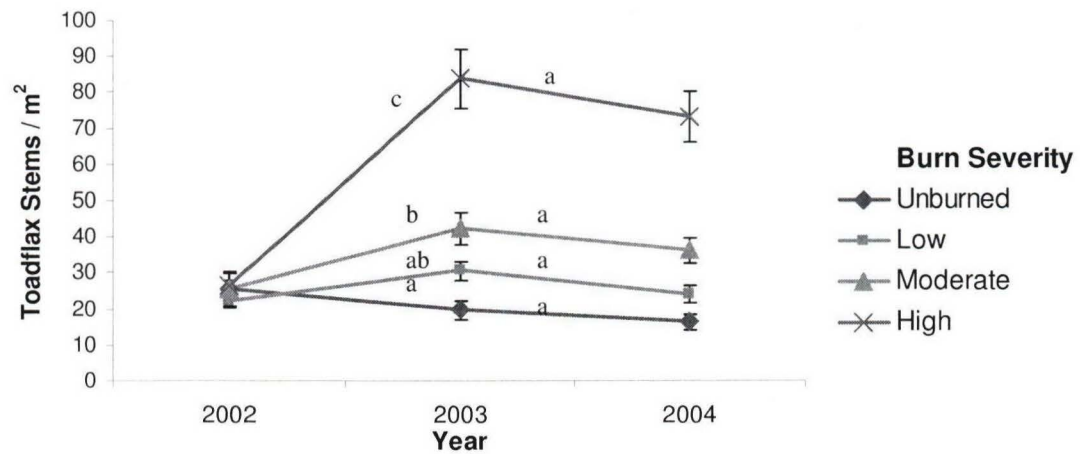


Figure 2. Average Dalmatian toadflax density stems per plot (no./m²), by year and burn severity class, and results of Tukey's HSD comparing the rate of change between burn severity classes, within each time step. Line segments within each time step labeled with the same letter did not differ significantly ($P > 0.025$).

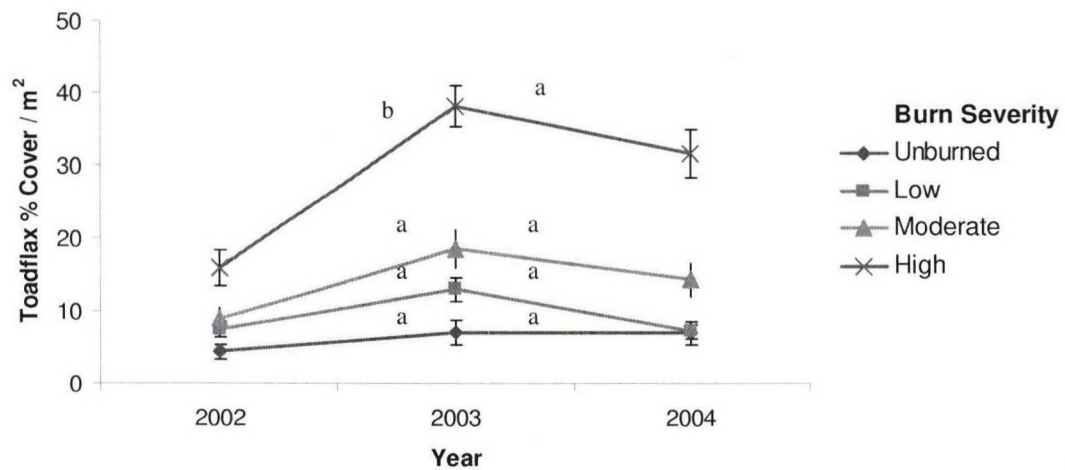


Figure 3. Average canopy cover (%) of Dalmatian toadflax, by year and burn severity class, and results of Tukey's HSD comparing the rate of change between burn severity classes, within each time step. Line segments within each time step labeled with the same letter did not differ significantly ($P > 0.025$).

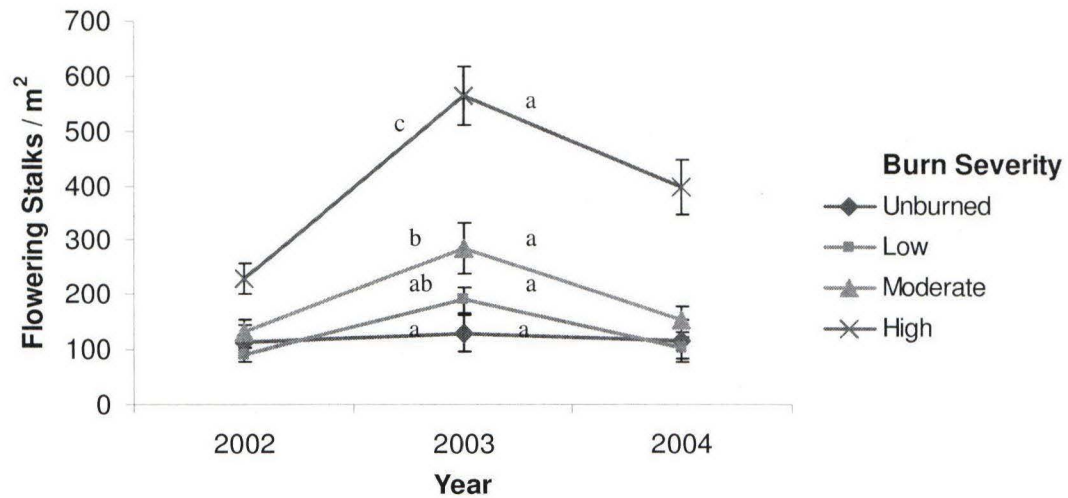


Figure 4. Average number of Dalmatian toadflax flowering stalks per plot (no./m²), by year and burn severity class, and results of Tukey's HSD comparing the rate of change between burn severity classes, within each time step. Line segments within each time step labeled with the same letter did not differ significantly ($P > 0.025$).

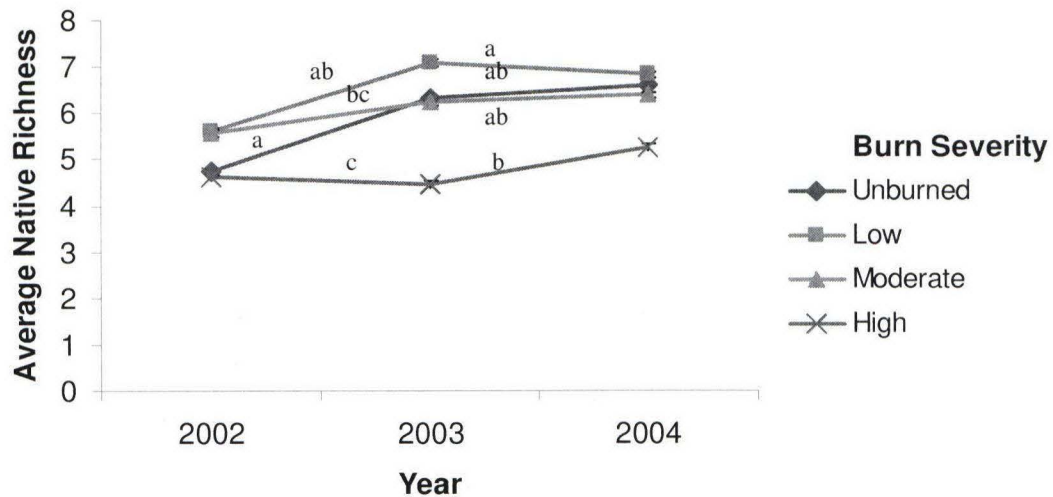


Figure 5. Average native species richness per plot (no. species/m²), by burn severity class and year and results of Tukey's HSD comparing the rate of change between burn severity classes, within each time step. Line segments within each time step labeled with the same letter did not differ significantly ($P > 0.025$).

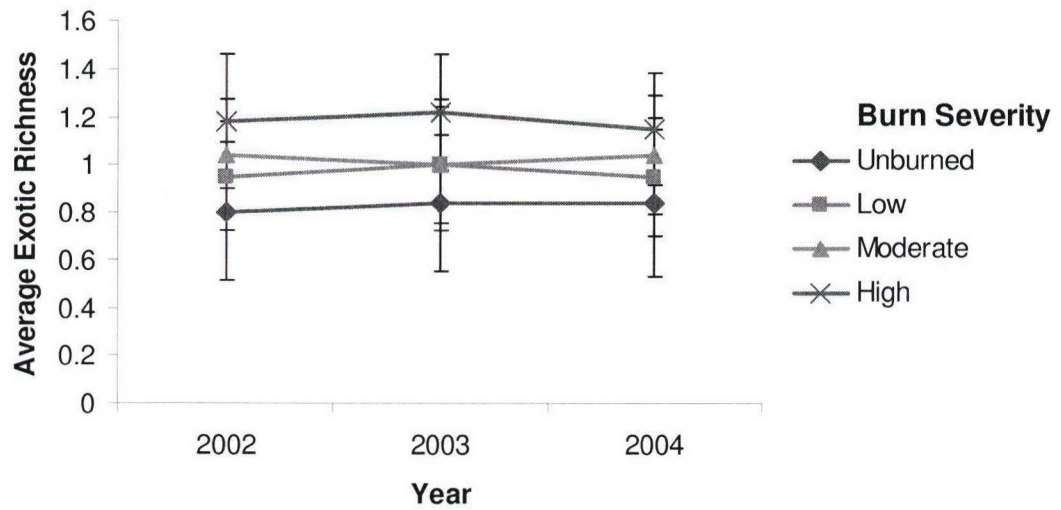
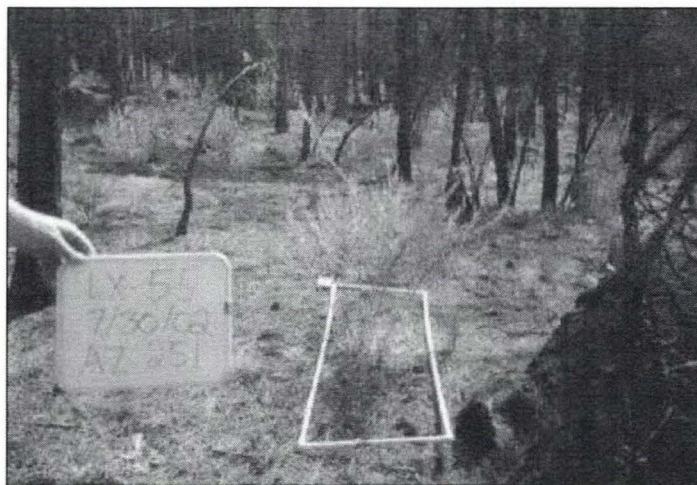
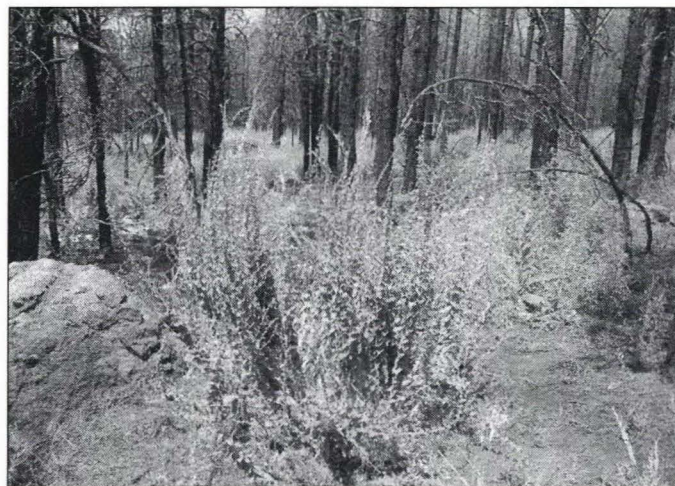


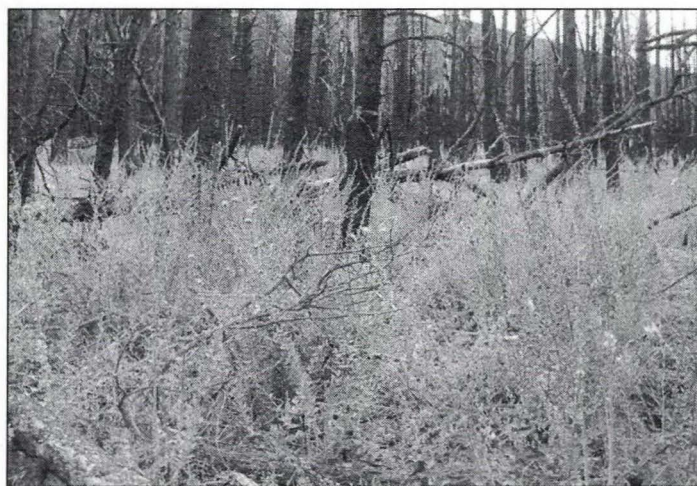
Figure 6. Average exotic species richness per plot (no. species/m²), by burn severity class and year.



a) 2002



b) 2003



c) 2004

Figure 7. Chronologic photographs taken of the same plot which shows Dalmatian toadflax spread outside of the plot frame

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CHAPTER 4

NATIVE SPECIES REVEGETATION: A SPECIES-BASED PERFORMANCE EVALUATION

Abstract

Federal, state, and local regulations increasingly require native species to be used for revegetating disturbed areas when it is possible. Sufficient growth and performance information is lacking for most native species and land managers are forced to make uninformed decisions about native species when developing a seed mix or to buy non-native seed mixes, for which information exists. We compared the germination, establishment, and growth traits of 28 native southwestern species to indicate their success in accomplishing revegetation goals. We conducted three types of seed performance trials: germination chamber, greenhouse, and field trials, and used this information in developing an integrated relative species performance rating. Annual ryegrass (*Lolium multiflorum* var. *gulf*), which is familiar to land managers, was included as a non-native comparison species. Six species had higher germination in the greenhouse over the growth chamber, and two species had higher germination in the field over the greenhouse. Warm season species performed better in the greenhouse than cool season species. Cool season species had higher average germination in all three trials, and higher cover and biomass production during the first field season than warm season species. Grass germination was only slightly higher than forbs in the field, but provided twice as much cover by the second field season. Root: shoot ratios were higher for cool season grasses and forbs than for warm season grasses and forbs. Species with the highest overall field performance ratings were *Elymus elymoides* (squirreltail), *Bouteloua gracilis* (blue grama), *Oxytropis lambertii* (purple locoweed), and *Bahia dissecta* (ragleaf bahia). The annual ryegrass did not perform better than some native grasses or forbs. The data on germination, first season and second season growth characteristics for 28 of native species allows federal and private land managers, as well as commercial landscapers and seed providers, to make informed decisions about revegetation strategies in this region.

Introduction

Revegetation through seeding is one of the most common and economically efficient practices used to restore large disturbed areas, and is the predominant post-fire rehabilitation method used by the U.S. Forest Service (Barro & Conard, 1987; Richards *et al.*, 1998; Robichaud *et al.*, 2000; Montalvo *et al.*, 2002). Revegetation to replace timber, increase forage, stabilize soil, and comparisons of seeding methods began in the late 1800's in the western United States, but often utilized non-native herbaceous plant species (Barro & Conard, 1987; Clary, 1989; Richards *et al.*, 1998; Robichaud *et al.*, 2000). Research on revegetating mine sites with native and non-native species has been extensive, but inherently focused on species able to tolerate post-mining soil conditions. Less attention has been given to using native species to stabilize soil, out-compete exotic plants, restore pre-disturbance biodiversity, and maintain local genetic integrity in native plant communities. Maintaining a diverse and self-sustaining plant community that will lead to the reestablishment of ecosystem composition and function, while maintaining genetic integrity, is the ultimate goal of ecological restoration, through revegetation. The purpose of this study was to provide baseline germination and growth data and relative performance ratings for a variety of native plant species characteristic of Arizona ponderosa pine (*Pinus ponderosa* P. & C. Lawson) communities.

Early efforts by the Forest Service used native species, but experimentation switched to exotic species because of their earlier emergence, high seed viability, easy establishment, rapid spread, ease of storage, and low cost over a short-term period (Barro & Conard, 1987; Robichaud *et al.*, 2000). Ryegrass (*Lolium multiflorum* Lam. or *L. perenne* L.) became the exotic species of choice in the 1940's for soil stabilization because of the mat-like growth pattern and dense, fibrous root system (Barro & Conard, 1987). Exotic species can have detrimental effects on ecosystems including reduced germination, growth, and cover of some native species, especially fire-followers, and suppression of woody species (Barro & Conard, 1987; Cione *et al.*, 2002). Non-native

species can create monocultures, convert shrublands to grasslands, reduce biodiversity, and reduce native genetic diversity and integrity through hybridization (Crane *et al.*, 1983; Barro & Conard, 1987; Clary, 1988; Schoennagel & Waller, 1999; Mortlock, 2000). Such changes in plant community composition and structure raise concerns about cascading effects on wildlife, insects, soil nutrient composition, and hydrology (Evans *et al.*, 2001; Korb & Springer, 2003).

Native species are advantageous because they are adapted to locally native environments and wildlife needs, have higher production, and usually contain a broader genetic base that can sustain itself over a long-term (Richards *et al.*, 1998; Mortlock, 2000). Revegetation with native species after weed-control can be a key factor in reducing reestablishment of exotics because native species can reduce opportunities for exotics by utilizing available resources on disturbed sites (Clary, 1988; Stohlgren *et al.*, 1999; Davis *et al.*, 2000; Cione *et al.*, 2002; Grieshop & Nowierski, 2002).

State and Federal laws have increasingly required revegetation with native species (Lippitt *et al.*, 1994). Federal agencies are required to restore disturbed areas using native seed and prevent introduction of exotic species (Executive Order # 13112 and Guiding Principles, February 3, 1999). Even with regulations, land managers commonly view the use of native species as a barrier and continue using non-native species due to lower cost, higher availability, or lack of information about natives (Barro & Conard, 1987; Richards *et al.*, 1998; Ken Moore, Bureau of Land Management, personal communication, 2/15/03; Dave Brewer, USFS, personal communication, 2/15/03). Past emphasis on exotic plant species has resulted in a wealth of information about several non-native species, but this knowledge base is sparse or non-existent for native species in most regions (Richards *et al.*, 1998; Montalvo *et al.*, 2002). The biological characteristics of southwestern native species that could be used for revegetation are poorly understood, and few studies have compared native and exotic species performance (Barro & Conard, 1987). Without data on performance of native species, land managers are forced to make uninformed decisions about developing a native seed mix versus buying non-native seed mixes (Barro & Conard, 1987; Richards *et al.*, 1998; Ken Moore,

Bureau of Land Management, personal communication, 2/15/03; Lauren Johnson, Kaibab National Forest, personal communication, 2/15/03; and Dave Brewer, USFS, personal communication, 2/15/03).

Factors affecting the performance of seeding efforts and plant establishment include choice of plant species, seed sources, soil attributes, seeding method, seed bed preparation, season, and seed bank longevity. This study explored the factors of species selection in the context of specific soil and environmental conditions and seeding methods. Specifically, we asked: 1) What are the germination, establishment, and growth traits of 28 native southwestern species that would indicate their success in accomplishing revegetation goals? and 2) How does native performance compare to a non-native annual ryegrass (*Lolium multiflorum* var. *gulf*) commonly used in revegetation? The goals for this study were to identify native species that have high germination, the ability to establish cover, provide above- and below-ground biomass, reproduce, and have the potential to stabilize soil. We conducted three types of seed plant performance trials: germination chamber, greenhouse, and field trials. The study included both cool and warm season, and annual and perennial grass and forb species.

We expected that germination would be highest in the germination chamber, second in the greenhouse, and lowest in the field trial, as conditions become increasing variable with each trial. *Iris missouriensis* (Rocky Mountain iris) was an exception; we expected higher germination in the second field season after a natural period of cold moist stratification. Grasses were expected to provide more cover and biomass than forbs. Based on revegetation studies, *L. multiflorum* var. *gulf* was expected to have the highest overall performance rating. Cool season species were expected to have higher germination and greater growth than warm season species in the first field season because some were ruderal species. The primary product of this study is a reference data set of germination and growth characteristics for a variety of native species. These data allow federal and private land managers, as well as commercial landscapers and seed providers, to make informed decisions about revegetation strategies in this region.

Methods

The term “native” varies between researchers, government entities, and environmental organizations and should be clearly defined prior to any revegetation project or research study. In this study, a species was considered native in Arizona according to Kearney and Peebles (1960).

Seed Source

Twenty-eight native southwestern herbaceous species and one non-native species were included in the study (Table 4.1). These species were chosen because they commonly occur in ponderosa pine stands in this region and viable seed was available. Seeds for 12 species were collected throughout spring and summer of 2002 at locations around northern Arizona. Seed production and viability was low in 2002 due to drought and collection of locally native species was limited. Commercial seed availability was also limited due to drought, but we were able to increase the number of species in the study by purchasing seed for 17 species, which were from locations outside of Arizona. Species were classified according to photosynthetic pathway and growing season (cool/warm) (Kearney & Peebles, 1960; Stubbendieck *et al.* 1986).

Seeds were stored in cloth soil bags and refrigerated at 4.4°C for 8 weeks to simulate natural cold treatment, break seed dormancy, and prevent insect attack. Although little information was available on the germination requirements for most species in the study, we assumed that some may require a period of cold stratification as a germination cue. Cold treatment is a common procedure and detrimental effects to species not requiring cold treatment have not been documented (Keeley, 1987). An additional sandpaper scarification treatment was applied to the species *Lupinus argenteus* Pursh in order to maximize germination for all trials. This species is known to respond to physical scarification (Lippitt *et al.*, 1994).

Environment

This study was conducted in 2003 and 2004, in Flagstaff, Arizona. The elevation is 2,134 m, average annual precipitation is 56.9 cm, and the monthly mean temperature ranges from -0.8°C to 16.2°C (54-year average, Table 4.2) (Western Regional Climate Center, 2004). Precipitation patterns are bimodal, characterized by periodic snow and rainfall in winter, followed by a pronounced drought in May and June, with late summer rains occurring in July and August (Sheppard *et al.*, 2002). The growing season is relatively short, ranging from 75-103 days depending on the specific elevation (Busco & Morin, 2003; Western Regional Climate Center, 2004). Ponderosa pine is the dominant forest vegetation type in northern Arizona, with a wide variety of grasses and forbs composing the understory. Quaking aspen (*Populus tremuloides* Michx), mixed conifer, and bristlecone pine (*Pinus aristata* Engelm.) can be found at higher elevations in northern Arizona, while pinyon-juniper (*Pinus edulis* Engelm. – *Juniperus spp.*) woodlands occur in surrounding lower elevations.

Soil

Due to the historic volcanic activity of the region most soils found in the northern Arizona ponderosa pine forest are derived from basalt and andesite parent material, with common soils being Inceptisols, Mollisols, and Alfisols, although sedimentary limestone parent material is not unusual (USDA Forest Service, 1995). Soil used in the study was local topsoil collected by a commercial supplier from the Rio de Flag drainage basin, east of downtown Flagstaff, AZ. and was used in the greenhouse and field trials. Soil macronutrient analysis was conducted to provide information about the specific growing conditions for this study. Before planting, 3 random soil core samples to a depth of 15 cm were collected and analyzed for total nitrogen, phosphorous, potassium, magnesium, calcium, percent organic matter, and pH (Table 4.3).

Germination Chamber Trial

Germination was defined as “the emergence and development from the seeds embryo of those essential structures which, for the kind of seeds in question, are indicative of the ability to produce a normal plant under favorable conditions” (Association of Official Seed Analysts, 1998). We defined germination as the emergence of the radical from the seed coat, at least 2 mm in length (Keeley, 1987; Doucet & Cavers, 1996).

We measured percent germination in a germination chamber (Percival model 1-35, Boise, Idaho). The temperature was set at 10°C nighttime and 23°C daytime with a photoperiod of 14 hours light and 10 hours dark to approximate the average natural photoperiod during July-September (Keeley & Pizzorno, 1986; Doucet & Cavers, 1996; Keeley, 1987; Western Regional Climate Center, 2004). For each species five 20-seed replicates were tested (n=5), totaling 100 seeds tested per species. Each 20-seed replicate was placed on 2 pieces of moistened filter paper in a plastic petri dish. Due to limited seed availability, only four 20-seed replicates (n=4), totaling 80 seeds were possible for *B. eupotroides*. The filter paper was kept moist by adding deionized water as needed (Association of Official Seed Analysts, 1998). Seed germination was checked every 2-3 days. Upon germination, emerging seedlings were tallied and removed from the dish. Seeds were allowed to germinate for 30 days or until 5 days passed without any germination recorded for that species (Keeley & Pizzorno, 1986; Keeley, 1987; Doucet & Cavers, 1996).

Greenhouse Trial

We filled ten 3.8-liter (1-gallon) black plastic pots with native top soil and planted 20 seeds per pot for each species; n=10 pots for each species. Seeds were buried 2 cm deep and spaced evenly from each other and the edge of the pot to reduce intra-specific competition after emergence. Planting occurred over two days at the end of May 2003 and pots were watered every 2-3 days in order to keep the soil moist. Five control pots of

unseeded soil were randomly arranged among the seeded pots to test for contamination of the soil by non-seeded plant species.

Seedling emergence was measured every 2-3 days for a minimum of 30 days following planting. After 30 days we manually thinned each pot to one individual plant per pot to remove competition, allowing the measurement of growth characteristics under optimal growing conditions. After a 93-day growing period (including the 30-day emergence period), based on the average length of the growing season, we measured basal and foliar cover (%), height, shoot length, root length, and total reproduction culms. All plants were then harvested, and roots were carefully washed and stored in a refrigerator until individuals were dried and weighed. All individual plants (separated by shoot and root parts) were placed in paper bags in an oven at 70°C for 48 hours, after which no weight change was detectible. Above-ground and below-ground samples were weighed separately to the nearest mg.

Field Trial

We constructed an above ground planter measuring 15 X 10 m and 30 – 46 cm deep using local top soil (described in greenhouse methods) to create a level surface with known soil characteristics. The planter border was created with XPotential Products landscaping ties, a recycled plastic composite, held in place with metal stakes. Using a planter versus direct planting in the ground removed slope effects and reduced contamination by plants that occurred in the area. To minimize mortality due to trampling and mammalian herbivory, a wire fence was erected around the study planter. The fence was 76 cm high with an additional 15 cm buried below the ground surface; the size of the fence openings was 1.3 x 1.3 cm.

The planter was divided into five, 1 X 15 m blocks, with 0.5-m wide pathways separating the blocks. To account for any unknown environmental variations of the study site we used a randomized block design, with each species replicated twice per block.

Each of the five blocks consisted of 60, 50- x 50-cm plots arranged in two rows with one species randomly assigned to each plot.

Planting occurred over two days in mid-July 2003 to coincide with the annual rainy season when seedling establishment is more likely to occur. One hundred seeds of a single species were planted in each plot, with an unseeded control randomly assigned to one plot. Seeds were placed on the soil surface, evenly spaced and away from the planter edge to reduce intra-specific competition, and then covered with 2 cm of soil. Throughout the duration of the study, weeds were removed from the planter to remove competition as a factor in this trial. Total growing time was from 10 July 2003 until the average first frost date on 21 September 2003 and 2004 (Western Regional Climate Center, 2004).

On-site precipitation was monitored with 4 rain gauges. When the amount of precipitation fell below the long-term weekly average, supplemental water was provided manually to match the long-term (54-year) average (Western Regional Climate Center, 2004). To test for a block effect on soil moisture, soil moisture was measured in 3 evenly distributed plots per row (6 per block) on 2 June 2004 using a Time Domain Reflectometer (TDR) (by Soil Moisture Equipment Corp., Goleta, CA).

Half of the plots (one row from each block) were measured and harvested at the end of one growing season (2003), while the remaining half was allowed to grow through a second season (2004). For each plot we measured percentage seedling emergence and foliar and basal cover (nearest 0.1%). We randomly chose six individual plants per plot to measure the following attributes at the end of the growing period: above-ground basal and foliar cover per individual (nearest 0.1%), height, shoot length, width, above-ground biomass, below-ground biomass, root-to-shoot ratio, and number of reproductive culms. At the end of the growing season, all plants were harvested, cleaned, roots and above-ground parts separated, placed in paper bags, dried and weighed. Plants were dried at 70°C for 48 hours, after which weight change was not detectable, and biomass was weighed to the nearest mg.

It was not possible to collect below-ground biomass after the second season due to extensive plant growth and the lack of below-ground boundaries between plots. Individuals of some grass species were difficult to distinguish during the second field season, so where necessary results are presented as total biomass per plot. If senescence occurred before the September harvest date, then the species were clipped early to avoid biomass loss. This clipping stimulated some species to resprout and the resprouted portions were measured and collected again at the final September clipping and held separately from the first clippings.

Species Field Performance Rating

We developed a field performance rating based on selected variables and the relative performance of each species. Total germination (%), cover (%) after one year, cover (%) after two years, total biomass after one year, and shoot biomass after two years were used to score each species. A score was calculated for each variable by dividing the observed value for a species by the best value observed within the same life form group. The scores were then averaged and multiplied by 100 to calculate an overall score that ranged from 1-100. The higher the overall score the better the species performed in comparison to the other study species.

Data Analysis

Data were summarized and descriptive statistics and standard errors were calculated for each measurement by species, and parametric statistics were calculated only to test for a block effect in the field. Percent emergence, mortality, and survivorship were calculated. Comparisons between species were based on the initial measurement of a plant and did not include the measurements of resprouting events. The statistical package JMP version 5.0.1.2 (JMP 5.0.1.2, 2003) was used to test for a block effect in the field trial on soil moisture and percent germination using an ANOVA. ANOVA

assumptions of normality and homogeneity of variance were tested by confirming the Shapiro-Wilk, and Levene's test statistics $\alpha > 0.05$.

Results

Germination Chamber Trial

Germination ranged from zero to 100%, with a mean of 54% (Table 4.4); unexpectedly, germination was not highest for all species in this trial. Six species with lower germination in the germination chamber than in the greenhouse were *Bouteloua curtipendula*, *Festuca arizonica*, *Pascopyron smithii*, and *Piptochateum pringelii*, *I. missouriensis*, and *Lupinus argenteus*. Germination results for growth types are as follows: 59.2% (cool season grass), 42.0% (warm season grasses), 44.6% (cool season forbs), and 84.2% (warm season forbs). Overall, forb germination was 54.4% and grass germination was 40.9%.

Greenhouse Trial

Overall, emergence, growth, and reproduction were greater in the greenhouse trial than in the field trial over both years (Table 4.4). Only two species had lower emergence in the greenhouse than the field: *Penstemon palmeri* and *Bahia dissecta*. Percent emergence of the non-native *L. multiflorum* var. *gulf* was $97.5 \pm 1.1\%$ which was higher than all native grasses. For warm season grasses, *Bouteloua gracilis* had the highest emergence with the least variability ($81 \pm 3.5\%$), and the cool season grass with the highest emergence was *F. arizonica* ($76 \pm 8.9\%$). The overall average emergence of cool season grasses was 52.9% and warm season grasses was 34.3%, excluding the non-native annual ryegrass. Emergence of cool season forbs (84.2%) was nearly twice that of warm season forbs (44.2%). The cool season forb with the highest percent emergence was *Vicia americana* (76.0%); and the warm season forb with the highest emergence was *Artemisia ludoviciana* (4.5%).

Foliar cover for *L. multiflorum* var. *gulf* (1.4%) was close to twice that of cool season (0.7%) and warm season (0.9%) grasses. On average the native grasses provided 1.0% foliar cover and forbs provided 0.8% cover per individual plant. However, the three legume species provided 1.0% average foliar cover per individual. The warm season grasses and forbs (0.7%) provided slightly more cover than the cool season grasses and forbs (0.6%). The cool season grass providing the greatest foliar cover was *F. arizonica* (0.3%); and the warm season grass with the greatest foliar cover was *Blepharoneuron tricolepis* (1.8%). The cool season forb providing the most foliar cover was *Brickellia eupatoroides* var. *chlorolepis* (1.6%); and the warm season forb providing the most foliar cover was *Machaeranthera canescens* (1.0%) (Table 4.5).

Eleven species reached reproductive maturity while in the greenhouse: *B. curtipendula*, *B. gracilis*, *L. multiflorum* var. *gulf*, *Muhlenbergia wrightii*, *Sporobolus cryptandrus*, *B. eupatoroides* var. *chlorolepis*, *B. dissecta*, *Linum lewisii*, *Senecio spartioides*, *Erigeron flagellaris*, and *Verbena macdougalii* (Table 4.5). *L. multiflorum* var. *gulf* had the highest culm production per plant.

Root: shoot ratios indicate the amount of biomass production allocated to above- and below-ground structures (Table 4.6). The root: shoot ratio for *L. multiflorum* var. *gulf* was 0.5. *Koeleria macrantha* (1.1) and *Blepharoneuron tricholepis* (0.8) the highest root: shoot ratio for warm and cool season grasses respectively. *V. americana* (1.1) and *Machaeranthera canescens* (0.7) had the highest root: shoot ratios for cool and warm season forbs respectively. Average root: shoot ratios were 0.7 (cool season grass), 0.6 (warm season grass), 0.6 (cool season forbs), and 0.5 (warm season forbs).

Total biomass production for *L. multiflorum* var. *gulf* was 1.9g. The cool season grass with the most biomass production was *P. smithii* (above and below-ground); the warm season grasses with the most biomass production were *Schizachyrium scoparium* (above-ground) and *B. tricolepis* (below-ground). *L. multiflorum* var. *gulf* did not provide more total biomass than native cool season grasses. The cool season forb with

the most biomass production was *S. spartioides*, and the warm season forb with the greatest biomass production was *A. ludoviciana* (Table 4.6). Native grasses (1.1g) did provide more total biomass than forbs (0.6g) and overall, the warm season grasses and forbs had more total biomass than the cool season grasses and forbs.

Field Trial

There was no significant block effect on soil moisture in the field trial so data were not analyzed by block (ANOVA, $p > 0.24$) and descriptive statistics were used. Seed contamination of the soil was not a significant concern. Only two foreign species occurred in the greenhouse trial, one was identified as the exotic *Salsola iberica*.

L. multiflorum var. *gulf* did not outperform natives with regard to percent emergence and foliar cover; though it was consistently among the top five grasses. *P. smithii*, *Elymus elymoides*, and *B. gracilis* performed well among all grass species for emergence, cover, and reproduction. The three legume species and *B. dissecta* had distinctly high % emergence and foliar cover among forbs. *P. palmeri* also had distinctly high emergence, but provided only minimal cover. After two field seasons, four grasses and three forbs reached reproductive maturity and *L. multiflorum* var. *gulf* was the only species to reproduce in both field seasons (Table 4.8).

Total emergence (both seasons additively) for cool season grasses was (19.4%), and warm season grasses was (5.1%). Total emergence for cool and warm season forbs was 11.7% and 3.9% respectively. Native grasses combined (11.1%) had a slightly higher average percent emergence than all forbs combined (9.0%). During the first field season, emergence for *L. multiflorum* var. *gulf* was 33.2%, which was higher than native cool season grasses, but not higher than warm season grasses. The cool season grass with highest emergence was *P. smithii* (38.8%), and the warm season grass with the highest emergence was *B. gracilis* (20.5%). The cool season forb with the highest emergence was *V. americana* (72.4%); and the warm season forb with the highest emergence was *B.*

dissecta (7.4%) (Table 4.4). These same species also had the highest total emergence after two field seasons.

After the first field season *L. multiflorum* var. *gulf* provided only 0.8% foliar cover, and average foliar cover for cool and warm season grasses was 1.0% and 0.3% respectively. By the second field season *L. multiflorum* var. *gulf* provided 15.3% foliar cover, and cool season grasses provided 4.0% and warm season grasses provided 5.6% foliar cover. In the first field season the greatest amount of foliar cover for all species was provided by *P. smithii* at 2.1%. *B. gracilis* had the highest foliar cover among all species after the second season, increasing from 0.6 % to 18.3% the second season (Table 4.7 and 4.8). *E. elymoides* (16.8%) provided the most foliar cover for cool season grasses in the second season.

In the first season *V. americana* (1.9%) provided the greatest cover among all forbs, and *B. dissecta* (0.3%) provided the most foliar cover for warm season forbs. During the second season, the cool season forb providing the most foliar cover was *Oxytropis lambertii* (12.6%); and the warm season forb providing the most foliar cover was *B. dissecta* (12.9%). Cool season forbs provided more foliar cover during both field seasons than warm season forbs, and native grasses consistently provided more foliar cover than forbs in both field seasons. After the first season grasses provided slightly more cover than forbs (0.5% and 0.4%), but doubled the forb cover after a second season, 4.8% and 2.4% respectively.

The root: shoot ratio was equal for cool and warm season grasses (0.6), but greater for cool season forbs (0.7) than warm season forbs (0.4). Therefore, the cool season forbs had a greater amount of below-ground production than the warm season forbs (Table 4.6). After the first season, species with the highest root: shoot ratio were *Koeleria macrantha* (cool grass), *B. tricholepis* (warm grass), *V. americana* (cool forb), and *M. canescens* (warm forb).

Total biomass production was greater for the cool season species than the warm season species after the first season. However, after the second season above-ground biomass of cool season grasses remained 3 times greater than warm season grasses; and above-ground biomass of cool season forbs was no longer greater than the warm season forbs. The total biomass production of native grasses was not greater than forbs after the first season; but above-ground biomass of grasses (2.5g) was twice that of forbs (1.3g) after the second field season. *L. multiflorum* var. *gulf* did not have more biomass production than native cool season grasses in either field season.

Biomass for *L. multiflorum* var. *gulf* was 0.04g in the first season and 9.9g in the second season. After the first field season, the cool season grass with the most biomass production was *E. elymoides* (0.07); and the warm season grass with the greatest biomass production was *B. curtipendula* (0.04). After the first field season the cool season forb with the greatest biomass production was *L. argenteus* (0.09g); and the warm season forb with the greatest biomass production was *B. dissecta* (0.014g) (Table 4.6). After the second field season, the cool season grass with the greatest above-ground biomass was *E. elymoides* (11.2g), and the warm season grass with the greatest above-ground biomass was *B. gracilis* (3.2g). After the second season the cool season forb with the most above-ground biomass was *O. lambertii* (2.9g), and the warm season forb with the most above-ground biomass was *B. dissecta* (4.6g) (Table 4.9).

Species Field Performance Rating

L. multiflorum var. *gulf* did not perform better than all of the native grasses. Overall, the annual ryegrass was the 3rd best performer among cool season grasses and 4th among all grasses. A relative performance rating was calculated for each species within the appropriate grouping for cool season grasses, warm season grasses, cool season forbs, and warm season forbs (Table 4.10). The species with the highest overall performance on a scale of 1-100 were *E. elymoides* (cool season grass), *B. gracilis* (warm season grass), *O. lambertii* (cool), *B. dissecta* (warm). In the first field season the cool season grasses and cool season forbs performed better than the warm season grasses and warm

season forbs with regard to germination, cover, and total biomass. Native grasses also consistently performed better than forbs in both field seasons. After the second season there was a switch where warm season grasses provided more cover than cool season grasses; and warm season forbs had greater biomass than cool season forbs.

Discussion

The indicators for overall performance addressed in this study were percent germination, ability to provide cover, to produce total biomass, and to produce below-ground biomass for soil stabilization. These indicators were compared both within and between life forms and photosynthetic pathways to identify species with high potential for revegetation.

Species Performance between Trials

The variable results between the three trials in this study highlight the differences between a germination chamber and the outdoor environment, and the importance of conducting an actual outdoor seed germination test. The primary reason for conducting germination chamber tests was to determine the percentage of viable seeds in a particular sample. A common procedure among managers is to use this percentage to calculate seeding density, and to decide whether or not to use a particular species for revegetation. However, results of this study indicate that some native species do not germinate well under germination chamber conditions, and emergence can be higher under greenhouse or field conditions. Contradicting our expectations, 6 of 28 (21%) species had higher germination in the greenhouse and one in the field than in the germination chamber. Furthermore, two species had higher germination in the field than the greenhouse. While lab germination tests can be good indicators for some species, they could also eliminate species that actually perform better under field conditions, such as *B. dissecta* in our study. Germination of *B. dissecta* in the greenhouse was poor (1.5%); however, it had higher germination in the field, and also provided the most cover, biomass, and

reproduction for late-season forbs. While the germination and growth of functional groups were not expected to be equal, we did expect trends to be similar between each trial. However, our between trial trends were not consistent. For example, germination chamber results also showed germination of warm season forbs to be greater than cool season forbs, which was reversed in the greenhouse trial. A germination chamber test alone is not adequate for all native species and rather, we advocate conducting field germination tests to determine the seeding density for a revegetation project.

The greenhouse trial in this study provided a baseline for comparing growth performance under presumed optimal conditions to harsher field conditions, but 2 species had higher emergence in the field than the greenhouse. A possible explanation for this is that greenhouse conditions did not provide these two species with the appropriate cues required for germination. Species receive different cues for germination through cold, moist stratification, fire scarification, or scarification by digestion from ungulates, precipitation patterns, temperature patterns, and soil attributes. It is unknown which environmental cues trigger each species and further investigation is warranted if the collective goal for revegetation practitioners is to increasingly use native species. Another use for greenhouse studies of native species is to indicate the performance a grower can expect if the objective is to grow native plugs for transplanting. The use of propagule plugs in revegetation can result in higher survivorship, rapid reproductive maturity, and increased plant size of seedlings than direct seeding (Busco, 2004; Steed, 2001). In some situations the use of transplants may be more cost efficient and ecologically effective than seeding, depending on the size of area treated, survivorship rates, and current cost associated with each method (Busco, 2004). Transplant plugs, however, are more difficult to apply to large areas or rugged terrain, are generally more expensive and time consuming, may require follow-up watering, and require a higher level of planning planting strategy (spatial distribution) than direct seeding (Lippitt *et al.*, 1994; Korb & Springer, 2003).

Seed Source

Seed source may have been a factor affecting species performance in the study, since some species were commercially grown while others were collected. Due to lack of information about many of the study species, we chose to include a high variety of species, rather than replicating seed sources for only a few species, and this may have favored those species which were commercially purchased. Some species did not perform well in any of the trials and collected seed had lower germination than commercial seed. This may be because collected seeds were exposed to variation in environmental conditions and herbivory before collection; and they were not cleaned and sorted to ensure a consistent and high amount of pure live seeds (PLS) per sample (Lippitt *et al.*, 1994; Korb & Springer, 2003). Some commercial seed companies also will collect seed from specified populations upon request or will grow out plants from collected seeds to produce large quantities of seed from a desired population, both of which are then sorted to produce higher PLS (Korb & Springer, 2003). *P. fendleriana* is an example of a collected species that had very low germination. After planting we discovered that the seeds had been infested with insects, which likely contributed to its low performance. Another species, *E. racemosum*, was commercially purchased and had very poor germination and performance. Attempts to increase germination by soaking seeds in boiled water and sandpaper scarification were not successful and we are unable to explain the poor performance. Managers should be aware that collected seed may have lower germination than commercial seed because collectors can not guarantee the same level of pure live seed as commercial growers without implementing screening measures. It is common practice for land managers to purchase seed commercially from growers in different states and ecotypes because the high volume demands are not being met by local growers, or a local grower does not exist. However, a local genetic strain from collected seed may perform better after germinating than a commercially grown variety. It would be beneficial for future studies to directly compare performance of collected versus commercial seed.

Soil Stabilization

Soil stabilization is one of the initial goals of revegetation and both above- and below-ground production are important in deterring soil erosion (Robichaud *et al.*, 2000). Above-ground cover protects soil from wind erosion, rain drop impact, and surface runoff while below-ground structures break up hydrophobic layers, increase pore space and water holding capacity, and prevent movement. In the field setting, grasses provided more above-ground cover than the forbs during both seasons, indicating that grasses provide more protection from surface erosion. Since the cool season grasses provided more cover initially, but warm season grasses had more cover after the second season, both types may play a role in successful long-term revegetation. Among forbs, the cool season forbs provided more cover than warm season forbs during both seasons. The annual ryegrass did not provide more cover or root biomass than 3 native grasses in the field and, therefore, provided less soil stabilization than the native grasses.

In the field *V. americana* had high germination and provided the greatest amount of root: shoot production, and may provide a high degree of soil stabilization. Cool season grasses and forbs overall had higher root: shoot ratios than warm season grasses and forbs, and could be used to provide soil stabilization during the spring snow melt. Since warm season grasses and forbs allocate more production to shoots later in the growing season, they were able to provide more foliar cover which may protect disturbed soil from late season rain. While these general ratios hold true when all species were grouped according to photosynthetic pathway, there were some distinct exceptions in our study. In the first field season, *P. smithii* (cool grass) and *O. lambertii* (cool forb) did not allocate more biomass production to roots (less than 40%), and in contrast provided the greatest above ground cover. Similarly, in the second season, *E. elymoides* (cool grass) and *O. lambertii* allocated less than 30% biomass to root production and provided the highest amount of above ground cover. These three species may be able to provide more aboveground cover early in the season than other cool season species.

Species Performance Rating

In the greenhouse environment, the exotic ryegrass performed better than all of the native grasses. However, in the field environment this did not hold true. Ryegrass performed well, as one of the top 5 grasses in the field, but was never the best performer for any of the measured variables. Species which received a better overall performance rating, *E. elymoides*, *P. smithii*, and *B. gracilis*, appear more appropriate to use in this region of the southwest than annual ryegrass. The only collected species which performed particularly well was the legume *O. lambertii*. Other forbs that performed well were the two legumes *L. argenteus* and *V. americana*, and *B. dissecta*. *O. lambertii* and *B. dissecta* also reproduced, suggesting they would be more likely to sustain production over time. Other studies in Northern Arizona also found that *E. elymoides*, *B. gracilis*, *L. argenteus* and other ruderal species performed well when seeded or on unseeded disturbed sites (Springer *et al.*, 2001; Elseroad, 2001; Korb, 2001; Crawford *et al.*, 2001). Contrastingly, Korb (2001) and Elseroad (2001) also found that *P. fendleriana* and *F. arizonica* performed well when seeded.

The overall performance rating (Table 4.10) reflects the relative performance of a species within its life form and photosynthetic pathway grouping. A manager could also use performance ratings for individual variables, to tailor their specific needs. The results of this study are preliminary in that they remain to be verified by another study or by seed from a different grower. Verification is particularly important for the collected species, and a study using commercially grown seed of the same species should be conducted.

Environmental Factors Affecting Species Performance

In arid high elevation regions, such as Flagstaff, plants must survive harsh living conditions including daily temperature swings of -1.1 – 4.4°C and regional droughts. Northern Arizona has been experiencing extreme drought conditions since 1996 (Western Regional Climate Center, 2004), and the late summer rains during this drought have been inconsistent, with a several days between rain events. The rainy season also provides

increased cloud cover and humidity, which greatly affects vegetation growth. We were able to provide supplemental water, but this was usually at times of low humidity and cloud cover. Our results can not account for effects related to an increased evapotranspiration and some species may have not germinated or performed poorly due to drought conditions, which may perform better in non-drought years. The field site was chosen to reflect a disturbed area with no direct overstory canopy and little indirect shade, since most revegetation occurs under these conditions. The amount of shade at a different site could cause variable results to be found, and shade-tolerant species to perform better (Naumburg & DeWald, 1999). Overall, we strove to create a field site which was representative of average growing conditions of disturbed, high elevation areas in northern Arizona, however, the results are site specific and site characteristics should be considered when choosing a seed mixture.

Choosing a Native Seed Mixture

Seed quality is the foundation of a successful revegetation project, so proper collection, process, and storage techniques should be followed to insure better germination (Lippitt *et al.*, 1994; Mortlock, 2000; Korb & Springer, 2003). In this study seed from commercial providers had better viability than collected seed, but did not have the local genetics preferred by restoration practitioners. In developing a seed mix it is important consider a suite of species that will be present all year in order to use available resources. We addressed this issue by including species that would sprout both early and late in the growing season, even if seeded at the same time. Seeding a mixture of both cool and warm season species that provide plant cover throughout the growing season may assist in reducing invasion by exotic species, enhancing wildlife habitat and forage, preventing soil erosion, and occupying resources year round. Studies have shown that a key mechanism for exotic species invasion, for species rich or species poor areas, is resource availability (Elton, 1958; Rejmanek', 1996; Sher & Hyatt, 1999; Davis *et al.*, 2000; Stohlgren *et al.*, 2001). Many disturbed areas have an excess of resources such as light, water, nutrients, and bare ground that if utilized by native species may help prevent the widespread establishment of non-native species that could hinder future restoration

efforts. A manager can occupy resources and space by choosing a native mix including grasses and forbs each represented by both cool and warm season species. From the species included in this study, we can recommend using the species with a high overall performance rating for the desired variables.

This site was protected from grazing and it is unknown how grazing would affect the overall response of species. Palatability of seeded species could affect grazing habits, growth and reproduction of plant species, and overall rate of recovery of the land. A mixture of palatable and non-palatable species may be desirable in order to provide forage while ensuring that a base level of vegetation remains. Seven species resprouted after clipping during the second field season, indicating that grazing may not negatively affect these species. Resprouting also may have occurred because plants were clipped too early, the plants senesced early and then resprouted with late rains, cooler temperatures in the late season, or because clipping stimulated growth. *O. lambertii*, *E. elymoides*, *P. smithii*, and *K. macrantha* each had more or almost equal growth in the short period after clipping than during the entire season.

The cost of purchasing seed is typically a limiting factor in determining species to be used in a revegetation project and the price of seed can also be highly variable year to year. Cost was not included as part of the overall performance rating for this study, and an average cost of seed for the study species in 2004 was calculated based on 3 seed companies (Table 4.1). Managers should consider cost when weighing the benefits and drawbacks of using more versus less expensive seed. It may be more ecologically beneficial to use expensive seed if it performs much better than the less expensive species.

Every revegetation project has unique attributes and challenges which managers must consider in the decision making process. The results of this study indicate that each group of species offers a significant contribution to meeting the goals of revegetation. Grasses and forbs and early or late season species play an important, but different, role in providing protection for disturbed land and reestablishing native plant communities. The

species-specific results presented in this study are an attempt to increase the knowledge base concerning southwestern native species so that land managers and commercial seed growers may knowledgably incorporate a diverse array of species in revegetation projects in this region.

Table 4. 1 List of plant species used in germination trials near Flagstaff, Arizona, and information on life form, life history strategy, photosynthetic pathway/growing season, and collection information. USDA Plants Database (2004) is the authority for scientific nomenclature.

Family Species	Life Form	Life History Strategy ¹	Photosynthetic Pathway/ Growing season	Collection Location/ Supplier ²	Cost Estimate \$/lb ⁵
Poaceae					
<i>Blepharoneuron tricholepis</i> (Torr.) Nash	Grass	P	warm	Collected: McMillan Mesa ⁴ Inside Flagstaff city limits	NA
<i>Bouteloua curtipendula</i> (Michx.) Torr.	Grass	P	warm	1	7.33
<i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths	Grass	P	warm	1	11.00
<i>Elymus elymoides</i> (Raf.) Swezey	Grass	P	cool	2	29.50
<i>Festuca arizonica</i> Vasey	Grass	P	cool	Collected: Hart Prairie ⁴ 24km N. of Flagstaff, AZ	21.00
<i>Koeleria macrantha</i> (Ledeb.) J.A. Schultes	Grass	P	cool	2	27.50
<i>Lolium multiflorum</i> var. <i>gulf</i> Lam.	Grass	A	cool	Warners Nursery	1.4
<i>Muhlenbergia wrightii</i> Vasey ex Coult.	Grass	P	warm	2	NA
<i>Pascopyrum smithii</i> (Rydb.) A. Löve	Grass	P	cool	2	6.33
<i>Piptochetium pringelii</i> (Beal) Parodi	Grass	P	warm	Collected: Dry Lake Hills ³ 7km N. of Flagstaff, AZ	NA

Family Species	Life Form	Life History Strategy ¹	Photosynthetic Pathway/ Growing season	Collection Location/ Supplier ²	Cost Estimate \$/lb ⁵
<i>Poa fendleriana</i> (Steud.) Vasey	Grass	P	cool	Collected: McMillan Mesa ⁴ Inside Flagstaff city limits	NA
<i>Schizachyrium scoparium</i> (Michx.) Nash	Grass	P	warm	2	10.80
<i>Sporobolus cryptandrus</i> (Torr.) Gray	Grass	P	warm	2	9.67
Asteraceae					
<i>Artemisia ludoviciana</i> Nutt.	Forb	P	warm	Collected: Mount Trumbull ³ 190km N. of Flagstaff, within Arizona Strip	92.5
<i>Bahia dissecta</i> (Gray) Britt.	Forb	A/B/P	warm	2	NA
<i>Brickellia eupatoroides</i> (L.) Shinners var. <i>chlorolepisa</i> (Woot. & Standl.) B.L. Turner	Forb/ subshrub	P	cool	Collected: Lonetree ³ Inside Flagstaff city limits	NA
<i>Erigeron flagellaris</i> Gray	Forb	B	cool	1	NA
<i>Erigeron speciosus</i> (Lindl.) DC.	Forb	P	warm	2	NA
<i>Machaeranthera canescens</i> (Pursh) Gray	Forb	A/P/B	warm	Collected: Flagstaff, AZ ³	NA
<i>Packera multilobata</i> (Torr. & Gray ex Gray) W.A. Weber & A. Löve	Forb	A/P	cool	Collected: Mount Trumbull ³ 190km N. of Flagstaff, within Arizona Strip	NA
<i>Senecio spartioides</i> Torr. & Gray	Forb/ subshrub	P	warm	Collected: Mount Trumbull ³ 190km N. of	NA

Family Species	Life Form	Life History Strategy ¹	Photosynthetic Pathway/ Growing season	Collection Location/ Supplier ² Flagstaff, within Arizona Strip	Cost Estimate \$/lb ⁵
Fabaceae					
<i>Lupinus argenteus</i> <u>Pursh</u>	Forb	P	cool	2 Collected: Abineau Trail ⁴ 18km N. Flagstaff, AZ	NA
<i>Oxytropis lambertii</i> <u>Pursh</u>	Forb	P	cool		NA
<i>Vicia Americana</i> <u>Muhl. ex</u> <u>Willd.</u>	Forb	P	cool	2	41.5
Iridaceae					
<i>Iris missouriensis</i> <u>Nutt.</u>	Forb	P	cool	Collected: Hart Prairie ⁴ 24km N. of Flagstaff	22.00
Linaceae					
<i>Linum lewisii</i> <u>Pursh</u>	Forb/ subshrub	P	cool	1	12.33
Polygonaceae					
<i>Eriogonum racemosum</i> <u>Nutt.</u>	Forb/ subshrub	P	cool	2	NA
Schrophulariaceae					
<i>Penstemon palmeri</i> <u>Gray</u>	Forb/ subshrub	P	cool	2	40.00
Verbenaceae					
<i>Verbena macdougalii</i> <u>Heller</u>	Forb	P	cool	Collected: Northern Arizona University ³ In Flagstaff, AZ	NA

¹P = perennial, B = biennial, A = annual²1 = Flagstaff Native Plant and Seed, AZ

2 = Western Native Seed, Coaldale, CO

⁴ Collected by Flagstaff Native Plant and Seed, AZ⁵ Average price of seed per pound based on 2-3 commercial seed producers in October 2004.

Family Species	Life Form	Life History Strategy ¹	Photosynthetic Pathway/ Growing season	Collection Location/ Supplier ²	Cost Estimate \$/lb ⁵
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³ Collected by Daniel Laughlin, Ecological Restoration Institute

Table 4.2 Total monthly precipitation (cm) and minimum and maximum temperatures (°C), compared to the long-term average (54 years) during the 2003 and 2004 growing seasons, in Flagstaff, Arizona (Western Regional Climate Center).

	Precipitation			Temperature (min, max)		
	Long-term average	2003 Actual ¹	2004 Actual ¹	Long-term average	2003 Actual	2004 Actual
May	1.8	NA	0	1.0, 19.8	2.8, 21.4	3.2, 21.4
June	1.3	NA	0	5.1, 25.6	5.9, 25.7	5.2, 25.9
July	6.2	2.7 ²	2.6	10.2, 27.7	11.9, 29.7	8.9, 27.3
August	7.2	11.5	12.5	9.5, 26.2	10.8, 25.7	9.1, 24.7
September	4.9	6.6 ³	0.9 ³	5.2, 23.3	6.3, 23.9	4.6, 22
Growing Season Total	21.4	20.83	16.02			

¹ Actual precipitation data during 2003 and 2004 was measured at the field site in Flagstaff, Arizona.

² Precipitation data for July 2003 was measured beginning on the planting date of 14 July.

³ Precipitation data for September was measured through the harvest date, 17 September.

Table 4.3. Macronutrient content for total nitrogen, phosphorous, potassium, magnesium, and calcium, plus organic matter content and pH of soil used in greenhouse and field germination tests of 29 plant species, in Flagstaff, Arizona. Analyses were conducted by the Northern Arizona University Analytical Services Lab operated by Dr. Tom Huntsberger.

Nutrient	Mean (S.E.)
Total Nitrogen (mgN/g)	0.4 (0.04)
Phosphorous (mgP/g)	0.9 (0.007)
Potassium (mgK/g)	5.6 (0.07)
Magnesium (mgMg/g)	9.9 (0.4)
Calcium (mgCa/g)	6.6 (0.2)
Organic Matter (%)	3.2 (0.07)
pH	7.7 (0.07)

Table 4.4. Percentage germination (standard error) of 29 species, by family, in a germination chamber, plus percentage emergence in greenhouse and field trials in Flagstaff, Arizona, in 2003 and 2004.

Growth Season Species	GERMINATION CHAMBER ¹	GREENHOUSE ²		FIELD	
	% Germination	30 Day % Emergence	Total % Emergence	% Emergence 2003	% Emergence 2004
Cool Season Grasses					
<i>Elymus elymoides</i>	93 (3.4)	76 (9.0)	76.5 (9.1)	25.8 (4)	0.8 (0.6)
<i>Festuca arizonica</i>	68 (4.9)	69.5 (5.4)	69.5 (5.4)	6.8 (1.6)	0.6 (0.4)
<i>Koeleria macrantha</i>	64 (8.0)	45 (4.7)	45 (4.7)	7.5 (1.8)	0.2 (0.2)
<i>Lolium multiflorum</i> var. <i>gulf</i>	99 (1)	97.5 (1.1)	97.5 (1.1)	33.2 (7.5)	0
<i>Pascopyrum smithii</i>	53 (6.44)	60.5 (5.1)	60.5 (5.1)	38.8 (6.5)	8.2 (3.6)
<i>Poa fendleriana</i>	18 (2.6)	0	13 (2.4)	6.0 (3.2)	2.4 (1.5)
Warm Season Grasses					
<i>Blepharoneuron tricholepis</i> ^a	29 (5.1)	14.5 (2.3)	14.5 (2.3)	4.3 (0.8)	0
<i>Bouteloua curtipendula</i> ^a	41 (7.0)	43 (4.0)	43 (3.4.0)	7.0 (0.8)	0
<i>Bouteloua gracilis</i>	87 (3.7)	81 (3.5)	81 (3.5)	20.5 (6.5)	0
<i>Muhlenbergia wrightii</i>	96 (1.9)	60.5 (7.4)	60.5 (7.4)	2.3 (0.8)	0
<i>Piptochetium pringelii</i>	12 (3)	15.5 (3.7)	15.5 (3.7)	0.1 (0.1)	0
<i>Schizachyrium scoparium</i> ^d	24 (3.7)	22.5 (3)	22.5 (3)	1.4 (0.5)	0
<i>Sporobolus cryptandrus</i>	5 (3.6)	3 (1.1)	3 (1.1)	0	0
Cool Season Forbs					
<i>Brickellia eupatoroides</i> var. <i>chlorolepis</i> ^b	60 (9.5)	49.5 (3.7)	49.5 (3.4)	0.01 (0.01)	0
<i>Erigeron flagellaris</i>	20 (1.6)	8.3 (2.5)	8.3 (2.5)	0	0
<i>Packera multilobata</i>	31 (4.9)	6 (1.3)	6 (1.3)	0.1 (0.1)	0
<i>Lupinus argenteus</i>	54 (4.3)	62 (3.8)	62 (3.2)	9.2 (2.7)	1.4 (0.8)
<i>Oxytropis lambertii</i>	18 (3)	7 (1.5)	7 (1.5)	11.8 (2.6)	15.1 (4.4)
<i>Vicia americana</i>	81 (4.8)	76 (2.6)	76 (2.6)	72.4 (5.0)	unk
<i>Iris missouriensis</i>	0	1 (0.7)	9.5 (2.3)	0.3 (0.2)	1.3 (0.3)
<i>Linum lewisii</i>	94 (3.7)	52.5 (7.2)	52.5	3.4 (1.9)	1.2 (0.6)
<i>Eriogonum racemosum</i> ^c	4 (1.9)	1 (0.7)	2 (0.8)	0	0.8 (0.8)

<i>Penstemon palmeri</i>	65 (3.2)	2 (0.8)	2.5 (0.8)	1.8 (0.9)	9.6 (1.9)
<i>Verbena macdougalii</i>	22 (5.1)	0.5 (0.5)	0.5 (0.5)	0	0.2 (0.2)
Warm Season Forbs					
<i>Artemisia ludoviciana</i>	81 (7.1)	4.5 (1.6)	4.5 (1.6)	0	0
<i>Bahia dissecta</i>	100 (6.8)	1.5 (0.8)	1.5 (0.8)	7.4 (1.1)	4.2 (1.36)
<i>Erigeron speciosus</i>	86 (4.3)	3.5 (1.1)	3.5 (1.1)	0	0
<i>Machaeranthera canescens</i>	82 (9.7)	4 (1.8)	4 (1.8)	0.7 (0.4)	3.0 (1.57)
<i>Senecio spartioides</i>	72 (10.2)	40 (6.5)	40 (6.5)	0.1 (0.1)	0

Note: Total emergence includes seedlings that emerged after the 30 day trial and after pots were thinned.

¹ Calculations based on 100 seeds.

² Calculations based on 200 seeds.

^a Based on greenhouse results, 150 seeds were used in field trial to ensure emergence.

^b Only 80 seeds were used for germination chamber and field trials, due to seed limitations.

^c Only 50 seeds were used for and field trials, due to seed limitations.

^d Based on greenhouse results, 200 seeds were used in field trial to ensure emergence.

Table 4.5. Average percent aerial and basal cover per individual plant, plus average height, shoot and root length, and number of flowering stalks (standard error) for 29 species, by family, in a greenhouse trial in Flagstaff, Arizona.

Growth Season Species	n	% Cover Aerial Individual	% Cover Basal Individu al	Height (cm)	Shoot Length (cm)	Root Length (cm) ^a	Flowering stalks/ mature plant
Cool Season Grasses							
<i>Elymus elymoides</i>	9	0.8 (0.1)	0.05 (0) 0.06	19.3 (2.2)	32.9 (3.5)		
<i>Festuca arizonica</i>	10	1.7 (0.3)	(0.01)	20.8 (2.05)	37.4 (1.6)		
<i>Koeleria macrantha</i>	10	0.9 (0.1)	0.1 (0.01)	12.6 (0.5)	15.3 (0.6)		
<i>Lolium multiflorum</i> var. gulf	10	1.4 (0.2)	0.1 (0.01) 0.07	25.5 (4.4)	31.4 (4.4)		77.5 (38.0)
<i>Pascopyrum smithii</i>	10	0.8 (0.2)	(0.02)	26.04 (3.7)	55.3 (1.6)		
<i>Poa fendleriana</i>	10	0.2 (0.09)	0.05 (0)	12.3 (0.8)	15.9 (1.8)		
<i>Blepharoneuron</i> <i>tricholepis</i> ^a	10	1.8 (0.3)	0.2 (0.02)	37.4 (6.02)	44.6 (4.5)		
Warm Season Grasses							
<i>Bouteloua</i> <i>curtipendula</i> ^a	10	1.0 (0.09)	0.07 (0.01) 0.08	46.7 (2.3)	78.5 (8.2)		52.5 (19.9)
<i>Bouteloua gracilis</i>	10	1.08 (0.1)	(0.01)	33.9 (3.4)	42.5 (3.4)		8 (3.0)
<i>Muhlenbergia wrightii</i>	10	0.4 (0.03)	0.05 (0)	15.0 (0.7)	20.3 (1.0)		3.9 (0.6)
<i>Piptochetium pringelii</i>	10	0.9 (0.1)	0.05 (0)	27.1 (3.3)	37.8 (3.3)		
<i>Schizachyrium</i> <i>scoparium</i> ^d	10	1 (0.1)	0.17 (0.02)	13.7 (1.6)	18.0 (1.7)		
<i>Sporobolus</i> <i>cryptandrus</i>	5	1.2 (0.2)	0.07 (0.01)	62.9 (5.5)	74.3 (6.01)		3.2 (0.67)
Cool Season Forbs							
<i>Brickellia</i> <i>eupatoroides</i> var.	10	1.6 (0.2)	0.05 (0)	18.1 (1.9)	42.3 (2.2)	30.9 (2.6)	5.2 (1.1)

<i>chlorolepis</i> ^b							
<i>Erigeron flagellaris</i>	6	0.5 (0.1)	0.05 (0)	4.9 (0.3)	6.05 (0.3)	23.7 (3.7)	4 (1)
			0.06				
<i>Packera multilobata</i>	10	0.9 (0.2)	(0.01)	5.3 (0.3)	7.6 (0.7)	41.7 (4.0)	
						37.02	
<i>Lupinus argenteus</i>	10	0.4 (0.09)	0.05 (0)	7.9 (0.7)	11.0 (1.07)	(4.5)	
			0.08				
<i>Oxytropis lambertii</i>	9	1.2 (0.3)	(0.01)	10.6 (1.4)	15.7 (1.6)	31.5 (6.2)	
						48.05	
<i>Vicia americana</i>	10	1.3 (0.1)	0.05 (0)	11.7 (1.1)	33.0 (2.43)	(4.7)	
			0.06				
<i>Iris missouriensis</i>	10	0.2 (0.03)	(0.01)	17.8 (2.2)	18.4 (2.2)	29.7 (5.3)	
			0.07				
<i>Linum lewisii</i>	10	0.8 (0.1)	(0.01)	28.2 (1.8)	31.1 (1.5)	30.6 (1.7)	13.5 (12.5)
<i>Eriogonum</i>							
<i>racemosum</i> ^c	3	0.2 (0.03)	0.05 (0)	2.6 (0.5)	5.1 (0.6)	8.1 (0.3)	
<i>Penstemon palmeri</i>	5	0.6 (0.2)	0.05 (0)	7.2 (1.5)	9.4 (2.0)	27.9 (7.1)	
<i>Verbena macdougalii</i>	1	0.4 (0)	0.05 (0)	44.6 (0)	44.7 (0)	33.7 (0)	39 (0)
Warm Season Forbs							
			0.08				
<i>Artemisia ludoviciana</i>	9	0.8 (0.2)	(0.02)	27.0 (3.8)	27.2 (3.8)		
<i>Bahia dissecta</i>	3	0.9 (0.2)	0.05 (0)	34.3 (14.7)	36.3 (13.4)	59 (16)	18 (3)
<i>Erigeron speciosus</i>	4	0.3 (0.02)	0.05 (0)	4.8 (0.6)	5.7 (0.6)	29.3 (2.6)	
<i>Machaeranthera</i>							
<i>canescens</i>	4	1.0 (0.05)	0.05 (0)	7.4 (0.7)	18.4 (2.1)	45.4 (9.1)	
<i>Senecio spartioides</i>	10	0.72 (0.06)	0.05 (0)	33.2 (1.9)	34.7 (1.9)	42.3 (3.5)	36.5 (5.05)

^a Root Length could not be accurately measured for species with net-like root systems

Table 4.6. Average shoot and root biomass per individual plant, plus the root: shoot ratio (standard error) for 29 species, by family, in a greenhouse and first season (2003) field trial in Flagstaff, Arizona.^{1,2}

Growth Season Species	GREENHOUSE				FIELD (2003)			
	n	Shoot Biomass (g)	Root Biomass (g)	Root: Shoot	n	Shoot Biomass (g)	Root Biomass (g)	Root: shoot (g)
Cool Season Grasses								
<i>Elymus elymoides</i>	9	0.9 (0.1)	0.7 (0.1)	0.8 (0.1)	113	0.05 (0.02)	0.02 (0.004)	0.4 (0.1)
<i>Festuca arizonica</i>	10	1.1 (0.1)	0.7 (0.1)	0.6 (0.1)	24	0.01 (0)	0.005 (0.001)	0.6 (0.1)
<i>Koeleria macrantha</i>	10	0.7 (0.1)	0.4 (0.1)	0.7 (0.1)	43	0.001 (0)	0.001 (0.002)	1.1 (0.2)
<i>Lolium multiflorum</i> var. <i>gulf</i>	10	1.1 (0.2)	0.8 (0.1)	0.9 (0.1)	63	0.03 (0.01)	0.01 (0.003)	0.5 (0.1)
<i>Pascopyrum smithii</i>	10	1.4 (0.2)	1.1 (0.1)	0.8 (0.1)	259	0.04 (0.01)	0.01 (0.003)	0.4 (0.05)
<i>Piptochetium pringelii</i>	10	0.8 (0.2)	0.3 (0.1)	0.6 (0.3)				
<i>Poa fendleriana</i>	10	0.1 (0.04)	0.02 (0.01)	0.6 (0.1)	44	0.002 (0)	0.001 (0.0002)	0.7 (0.1)
Warm Season Grasses								
<i>Blepharoneuron</i> <i>tricholepis</i>	10	1.8 (0.4)	0.8 (0.1)	0.5 (0.1)	20	0.01 (0)	0.007 (0.002)	0.8 (0.1)
<i>Bouteloua curtipendula</i>	10	1.5 (0.2)	0.7 (0.1)	0.5 (0.03)	32	0.03 (0)	0.01 (0.004)	0.4 (0.04)
<i>Bouteloua gracilis</i>	10	1.3 (0.3)	0.6 (0.1)	0.5 (0.1)	118	0.01 (0)	0.006 (0.002)	0.5 (0.1)
<i>Muhlenbergia wrightii</i>	10	0.2 (0.01)	0.1 (0.01)	0.8 (0.04)	13	0.01 (0)	0.007 (0.003)	0.8 (0.2)
<i>Schizachyrium scoparium</i>	10	1.7 (0.2)	1.1 (0.2)	0.7 (0.1)	12	0.01 (0)	0.007 (0.003)	0.6 (0.1)
<i>Sporobolus cryptandrus</i>	5	3.1 (0.6)	0.8 (0.1)	0.3 (0.04)				
Cool Season Forbs								
<i>Brickellia eupatorioides</i> var. <i>chlorolepis</i>	10	0.9 (0.1)	0.5 (0.1)	0.8 (0.1)	1	0.02 (0)	0.03 (0)	1.1 (0)
<i>Erigeron flagellaris</i>	6	0.2 (0.04)	0.04 (0.02)	0.2 (0.1)				
<i>Eriogonum racemosum</i>	3	0.1 (0.02)	0.1 (0.01)	0.2 (0.0)				
<i>Iris missouriensis</i>	10	0.1 (0.04)	0.1 (0.04)	0.8 (0.1)				
<i>Linum lewisii</i>	10	0.9 (0.1)	0.7 (0.06)	0.8 (0.08)	26	0.01 (0.01)	0.004 (0)	0.8 (0.3)
<i>Lupinus argenteus</i>	10	0.2 (0.03)	0.2 (0.04)	1.2 (0.2)	12	0.06 (0.01)	0.03 (0.01)	0.5 (0.04)
<i>Packera multilobata</i>	10	0.6 (0.1)	0.3 (0.1)	0.5 (0.1)				

<i>Penstemon palmeri</i>	5	0.5 (0.3)	0.2 (0.1)	0.3 (0.06)	4	0.003 (0)	0.001 (0)	0.4 (0)
<i>Oxytropis lambertii</i>	9	1 (0.2)	0.2 (0.1)	0.2 (0.02)	53	0.03 (0.01)	0.008 (0)	0.2 (0.1)
<i>Verbena macdougalii</i>	1	1.3 (0)	0.6 (0)	0.4				
<i>Vicia americana</i>	10	0.5 (0.1)	0.6 (0.1)	1.3 (0.1)	304	0.02 (0)	0.02 (0.01)	1.1 (0.2)
Warm Season Forbs								
<i>Artemisia ludoviciana</i>	9	1.3 (0.27)	0.9 (0.3)	0.6 (0.1)				
<i>Bahia dissecta</i>	3	0.9 (0.4)	0.2 (0.1)	0.2 (0.02)	30	0.01 (0)	0.004 (0)	0.3 (0.05)
<i>Erigeron speciosus</i>	4	0 (0.01)	0.004 (0)	0.6 (0.1)				
<i>Machaeranthera</i>								
<i>canescens</i>	4	0.9 (0.1)	0.2 (0.03)	0.8 (0.1)	2	0.002 (0)	0.001(0)	0.7 (0)
<i>Senecio spartioides</i>	10	1.1 (0.1)	0.7 (0.1)	0.7 (0.1)	1	0.05 (0)	0.01 (0)	0.3 (0)

1. Species with zero emergence (Table 4) have been excluded from this table.
2. An empty cell indicates that there was no emergence and no data was collected for that cell.

Table 4.7. Average percent aerial and basal cover per plot, plus average shoot height, shoot width, root length (standard error) for 29 species, by family, in a first season field trial in Flagstaff, Arizona .

Growth Season Species	n	Aerial % Cover Plot	Basal % Cover Plot	n	Height Individual (cm)	Width Individual (cm)	Length Individual (cm)
Cool Season Grasses							
<i>Elymus elymoides</i>	5	1.5 (0.9)	0.1 (0.04)	30	10.8 (0.7)	10.2 (1.04)	12.7 (0.6)
<i>Festuca arizonica</i>	4	0.1 (0.05)	0.05 (0)	19	5.6 (0.9)	1.6 (0.4)	6.0 (0.8)
<i>Koeleria macrantha</i>	4	0.05 (0)	0.05 (0)	23	1.6 (0.3)	1.2 (0.2)	1.8 (0.2)
<i>Lolium multiflorum</i> var. gulf	5	0.8 (0.5)	0.1 (0.04)	26	5.7 (0.6)	6.4 (1.4)	7.6 (1.0)
<i>Pascopyrum smithii</i>	5	2.1 (0.5)	0.1 (0.03)	30	9.02 (0.7)	8.04 (1.4)	10.6 (1.01)
<i>Poa fendleriana</i>	4	0.06 (0.01)	0.05 (0)	14	2.7 (0.5)	0.7 (0.6)	3.3 (0.4)
Warm Season Grasses							
<i>Blepharoneuron</i> <i>tricholepis</i>	5	0.2 (0.03)	0.05 (0)	26	3.0 (0.4)	3.8 (0.4)	3.6 (0.4)
<i>Bouteloua curtipendula</i>	5	0.4 (0.1)	0.06 (0.01)	28	6.9 (0.7)	8.2 (0.9)	9.6 (1.0)
<i>Bouteloua gracilis</i>	5	0.6 (0.3)	0.06 (0.01)	22	2.3 (0.2)	3.4 (0.4)	2.9 (0.3)
<i>Muhlenbergia wrightii</i>	3	0.1 (0.04)	0.05 (0)	12	3.6 (0.6)	3.0 (0.3)	4.06 (0.6)
<i>Schizachyrium scoparium</i>	4	0.1 (0.03)	0.05 (0.05)	12	2.4 (0.3)	3.4 (0.5)	3.1 (0.3)
Cool Season Forbs							
<i>Brickellia eupatoroides</i> var. <i>chlorolepis</i>	1	0.2 (0)	0.05 (0)	1	4.3 (0)	3.4 (0)	4.9 (0)
<i>Linum lewisii</i>	4	0.09 (0.02)	0.05 (0)	12	3.01 (0.5)	1.5 (0.3)	3.5 (0.6)
<i>Lupinus argenteus</i>	5	0.31 (0.06)	0.05 (0)	12	4.4 (0.5)	4.9 (0.6)	5.1 (0.5)
<i>Oxytropis lambertii</i>	5	0.6 (0.2)	0.06 (0.01)	29	3.4 (0.3)	2.7 (0.3)	3.9 (0.3)
<i>Penstemon palmeri</i>	1	0.1 (0)	0.05 (0)	3	0.4 (0.2)	1.03 (0.6)	0.7 (0.4)
<i>Vicia americana</i>	5	1.9 (0.3)	0.09 (0.04)	30	3.8 (0.3)	3.4 (0.3)	4.6 (5.3)
Warm Season Forbs							
<i>Bahia dissecta</i>	5	0.3 (0.08)	0.05 (0)	25	1.4 (0.1)	2.5 (0.3)	2.1 (0.2)
<i>Machaeranthera</i>	1	0.1 (0)	0.05 (0)	2	0.7 (0.1)	1.05 (0.2)	0.9 (0.1)

*canescens**Senecio spartioides*

1

0.3 (0)

0.05 (0)

1

5.1 (0)

5.8 (0)

5.5 (0)

Note:

Species with zero emergence (Table 4) have been excluded from this table.

Table 4.8. Average percent aerial and basal cover per plot, plus average height, shoot and root length, and number of flowering stalks (standard error) for 29 species, by family, in a second season field trial in Flagstaff, Arizona.^{1,2,3}

Growth Season Species	n	Aerial % Cover Plot	Basal % Cover Plot	n	Height Individual (cm)	Width Individual (cm)	Shoot Length (cm)	# of Seed Heads
Cool Season Grasses								
<i>Elymus elymoides</i>	5	16.8 (8.8)	0.6 (0.4)	27	19.4 (2.5)	14.4 (2.9)	19.9 (2.6)	18.7 (7.0)
<i>Elymus elymoides</i> (resprouts)	4	19.8 (13.5)	0.7 (0.2)	22	16.9 (0.9)	17.3 (1.7)	18.9 (1.0)	
<i>Festuca arizonica</i>	5	0.4 (0.2)	0.03 (0.02)	14	5.9 (0.62)	3.4 (0.4)	6.5 (0.5)	
<i>Festuca arizonica</i> (resprouts)	1	0.5 (0)	0.2 (0)	2	7.9 (0.4)	4.9 (0.05)	8 (0.3)	
<i>Koeleria macrantha</i>	5	0.3 (0.2)	0.05 (0.04)	10	2.5 (0.5)	3.2 (0.8)	3.05 (0.5)	
<i>Koeleria macrantha</i> (resprouts)	1	0.7 (0)	0.2 (0)	2	3.1 (0)	5.4 (1.1)	3.8 (0)	
<i>Lolium multiflorum</i> var. gulf	5	15.3 (13.7)	0.3 (0.2)	16	31.9 (2.7)	0 (0)	34.3 (3.05)	12.8 (7.8)
<i>Pascopyrum smithii</i>	5	1.3 (0.4)	0.2 (0.06)	29	15.6 (1.9)	7.1 (0.9)	17.0 (2.0)	2.7 (1.2)
<i>Pascopyrum smithii</i> (resprouts)	4	13.6 (12.2)	0.4 (0.2)	15	15.7 (1.5)	13.8 (2.7)	17.09 (1.7)	
<i>Poa fendleriana</i>	5	1.4 (0.5)	0.3 (0.2)	4	3.9 (1.0)	2.7 (0.3)	4.6 (0.9)	
Warm Season Grasses								
<i>Blepharoneuron</i> <i>tricholepis</i>	4	6.5 (1.7)	0.6 (0.1)	21	12.7 (1.7)	12.2 (1.08)	13.8 (1.7)	
<i>Bouteloua</i> <i>curtipendula</i>	3	1.3 (0.6)	0.2 (0.03)	7	12.6 (2.4)	11.4 (2.8)	14.1 (2.7)	
<i>Bouteloua gracilis</i>	4	18.3 (17.3)	0.7 (0.4)	19	4.7 (0.4)	7.07 (0.7)	5.9 (0.51)	
<i>Muhlenbergia</i> <i>wrightii</i>	2	1.5 (0.5)	0.4 (0.2)	4	10.9 (2.7)	6.4 (1)	10.0 (3.7)	
<i>Schizachyrium</i> <i>scoparium</i>	2	0.4 (0.1)	0.1 (0)	2	3.6 (1.6)	4.5 (2.3)	3.7 (1.6)	

<i>Schizachyrium scoparium</i> (resprouts)	1	0.2 (0)	0.1 (0)	1	3.4 (0)	3.1 (0)	3.5 (0)	
Cool Season Forbs								
<i>Linum lewisii</i>	2	0.6 (0.4)	0.4 (0.3)	5	7.0 (1.8)	2.3 (0.6)	7.2 (1.8)	
<i>Lupinus argenteus</i>	4	0.8 (0.1)	0.1 (0)	11	6.0 (0.6)	6.07 (1.3)	7.3 (0.9)	
<i>Lupinus argenteus</i> (resprouts)	1	0.7 (0)	0.1 (0)	7	3.6 (0.7)	3.3 (0.8)	4.2 (0.8)	
<i>Oxytropis lambertii</i>	5	4.7 (3.8)	0.3 (0.2)	21	50.7 (42.8)	5.8 (0.6)	8.3 (0.9)	2 (0)
<i>Oxytropis lambertii</i> (resprouts)	5	12.6 (9.2)	0.42 (0.2)	20	8.2 (0.6)	9.2 (1.04)	9.1 (0.7)	
<i>Oxytropis lambertii</i> (seedlings) ^a	8	0.4 (0.1)	0.1 (0.01)	34	1.3 (0.1)	0.9 (0.07)	1.5 (0.1)	
<i>Packera multilobata</i>	1	1 (0)	0.1 (0)	1	3.1 (0)	1.05 (0)	3.5 (0)	
<i>Penstemon palmeri</i>	5	0.2 (0.07)	0.1 (0)	11	1.6 (0.2)	1.6 (0.3)	1.9 (0.2)	
<i>Verbena macdougalii</i>	1	0.2 (0)	0.1 (0)	1	1.2 (0)	2.4 (0)	2.1 (0)	
<i>Vicia americana</i>	5	1.06 (0.2)	0.06 (0.02)	25	5.0 (0.3)	2.9 (0.5)	6.06 (0.4)	
<i>Vicia americana</i> (resprouts)	4	0.5 (0.2)	0.08 (0.03)	13	3.6 (0.4)	2.9 (0.4)	4.1 (0.5)	
Warm Season Forbs								
<i>Bahia dissecta</i>	5	12.9 (5.1)	0.6 (0.2)	28	7.6 (1.5)	6.3 (0.6)	8.5 (1.7)	
<i>Machaeranthera canescens</i>	4	2.3 (1.09)	0.3 (0)	13	10.4 (4.03)	5.5 (0.9)	11.7 (4.4)	

Notes:

^a After the initial clipping, OXYLAM seedlings emerged and were collected separately.

1. An empty cell indicates that the variable could not accurately be measured.
2. Species with zero percent emergence (Table 4) have been excluded from this table.
3. Many species resprouted after the initial clipping; resprouts were measured again the final clipping in September.

Table 4.9. Above-ground biomass (standard error) production in the second growing season (2004) for 29 species, by family, in a field trial in Flagstaff, Arizona.

Growth Season	Species	N = plot	Shoot Biomass (g/m²)
Cool Season Grasses			
	<i>Elymus elymoides</i>	5	11.2 (4.2)
	<i>Elymus elymoides</i> (resprout)	5	3.6 (1.2)
	<i>Festuca arizonica</i>	5	0.1 (0.06)
	<i>Festuca arizonica</i> (resprout)	1	0.04 (0)
	<i>Koeleria macrantha</i>	4	0.3 (0.2)
	<i>Koeleria macrantha</i> (resprout)	1	0.8 (0)
	<i>Lolium multiflorum</i> var. <i>gulf</i>	4	9.9 (5.4)
	<i>Pascopyrum smithii</i>	5	3.9 (1.7)
	<i>Pascopyrum smithii</i> (resprout)	4	1.6 (1.08)
Warm Season Grasses			
	<i>Blepharoneuron tricholepis</i>	4	2.2 (0.5)
	<i>Bouteloua curtipendula</i>	2	0.8 (0.3)
	<i>Bouteloua gracilis</i>	4	3.2 (2.3)
	<i>Muhlenbergia wrightii</i>	2	0.5 (0.2)
	<i>Schizachyrium scoparium</i>	1	0.03 (0)
	<i>Schizachyrium scoparium</i> (resprout)	1	0.06 (0)
Cool Season Forbs			
	<i>Linum lewisii</i>	2	0.2 (0.2)
	<i>Lupinus argenteus</i>	5	1.0 (0.3)
	<i>Lupinus argenteus</i> (resprout)	1	0.6 (0)
	<i>Oxytropis lambertii</i>	5	3.2 (1.34)
	<i>Oxytropis lambertii</i> (resprout)	5	2.4 (1.02)
	<i>Oxytropis lambertii</i> (seedling) ^a	9	0.1 (0.03)
	<i>Packera multilobata</i>	1	0.7 (0)
	<i>Penstemon palmeri</i>	6	0.3 (0.3)
	<i>Verbena macdougalii</i>	1	0.02 (0)
	<i>Vicia americana</i>	5	0.5 (0.7)
	<i>Vicia americana</i> (resprout)	4	0.06 (0.02)
Warm Season Forbs			
	<i>Bahia dissecta</i>	5	4.6 (1.7)
	<i>Machaeranthera canescens</i>	5	0.7 (0.6)

Notes:

^a After the initial clipping, *O. lambertii* seedlings emerged and were collected separately.

1. Species with percent emergence (Table 4) have been excluded from this table.

2. Many species resprouted after the initial clipping; resprouts were collected again at the final clipping in September.

Table 4.10. Relative species performance rating of 29 species, by photosynthetic pathway, for the field trial, including ratings for percent cover (2003 and 2004), total germination, total biomass (2003), shoot biomass (2004), and overall performance rating.

Growth Season	% Cover/ plot 2003	% Cover/ plot 2004	Total % Germination	Total Biomass 2003 (g)	Shoot Biomass 2004 (g)	Overall Rating (1-100)
Species						
Cool Season						
Grasses						
<i>Elymus</i>						
<i>elymoides</i>	0.72	1.00	0.39	1.00	1.00	82
<i>Festuca</i>						
<i>arizonica</i>	0.05	0.02	0.01	0.23	0.01	6
<i>Koeleria</i>						
<i>macrantha</i>	0.02	0.02	0.01	0.04	0.02	2
<i>Lolium</i>						
<i>multiflorum</i> var.						
<i>gulf</i>	0.38	0.91	0.34	0.59	0.88	62
<i>Pascopyrum</i>						
<i>smithii</i>	1.00	0.08	1.00	0.78	0.34	64
<i>Poa fendleriana</i>	0.03	0.09	0.18	0.06	0.00	7
Warm Season						
Grasses						
<i>Blepharoneuron</i>						
<i>tricholepis</i>	0.33	0.36	0.33	0.38	0.69	42
<i>Bouteloua</i>						
<i>curtipendula</i>	0.64	0.07	0.08	1.00	0.25	41
<i>Bouteloua</i>						
<i>gracilis</i>	1.00	1.00	0.92	0.44	1.01	88
<i>Muhlenbergia</i>						
<i>wrightii</i>	0.22	0.08	0.08	0.41	0.17	19
<i>Piptochetium</i>						
<i>pringelii</i>	0.00	0.00	0.00	0.00	0.00	0
<i>Schizachyrium</i>						
<i>scoparium</i>	0.20	0.02	0.07	0.40	0.01	14
<i>Sporobolus</i>						
<i>cryptandrus</i>	0.00	0.00	0.00	0.00	0.00	0
Cool Season Forbs						
<i>Brickellia</i>						
<i>eupatoroides</i>						
var. <i>chlorolepis</i>	0.08	0.00	0.00	0.58	0.00	13
<i>Erigeron</i>	0.00	0.00	0.00	0.00	0.00	0

<i>flagellaris</i>						
<i>Packera</i>						
<i>multilobata</i>	0.00	0.21	0.00	0.00	0.23	9
<i>Lupinus</i>						
<i>argenteus</i>	0.17	0.18	0.02	1.00	0.30	33
<i>Oxytropis</i>						
<i>lambertii</i>	0.29	1.09	0.08	0.48	1.01	59
<i>Vicia americana</i>	1.00	0.23	0.04	0.54	0.15	39
<i>Iris</i>						
<i>missouriensis</i>	0.00	0.00	0.02	0.00	0.00	0
<i>Linum lewisii</i>	0.48	0.13	0.06	0.16	0.07	18
<i>Eriogonum</i>						
<i>racemosum</i>	0.00	0.00	0.01	0.00	0.00	0
<i>Penstemon</i>						
<i>palmeri</i>	0.05	0.05	0.16	0.05	0.10	8
<i>Verbena</i>						
<i>macdougalii</i>	0.00	0.04	0.00	0.00	0.01	1
Warm Season Forbs						
<i>Artemisia</i>						
<i>ludoviciana</i>	0.00	0.00	0.00	0.00	0.00	0
<i>Bahia dissecta</i>	1.00	1.00	1.00	0.00	1.01	80
<i>Machaeranthera</i>						
<i>canescens</i>	0.40	0.17	0.32	0.04	0.15	22
<i>Erigeron</i>						
<i>speciosus</i>	0.00	0.00	0.00	0.00	0.00	0
<i>Senecio</i>						
<i>spartioides</i>	1.00	0.00	0.01	1.00	0.00	40

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CHAPTER 5

MANAGEMENT IMPLICATIONS

Our findings have direct implications for land managers, scientists, conservation organizations, and lay people who are involved in ecological restoration, conservation, and weed control in the ponderosa pine forest of the southwest United States. Land management recommendations based on results of my studies should be placed in the specific context of each weed control or revegetation project in which they are applied.

We found increased growth and reproduction of the exotic, invasive species Dalmatian toadflax (*Linaria dalmatica*) at all burn severity classes in the Leroux Fire. The decrease of toadflax variables reported in the third year of this study should not be interpreted as an indication that Dalmatian toadflax is declining, but rather that plants are spreading outward from a central parent plant location. Fire was the significant driver of toadflax increase between 2002 and 2003, presumably allowing it to take advantage of excess available resources and reduced native competition until it reached a maximum critical density threshold. In the subsequent year, toadflax density became the driving force for a decline of toadflax within plots between 2003 and 2004 and a spread outside of plots. Mean toadflax stem density, cover and reproduction were all highest in the high burn severity and decreased with decreasing burn severity, indicating the toadflax production is directly related to the degree of change in the post-fire environment. Low toadflax density plots also experienced the greatest increase in toadflax over time.

Therefore, this study indicates that higher burn severity and lower density areas are candidates for rapid toadflax invasion and spread, so control efforts may be more efficient when focused on these areas. Since toadflax occurs at a low density along the edge of larger dense patches, it may be logical to concentrate at this patch periphery and work toward the center over time. This method is increasingly important for larger patches. For example, if a manager has limited funding and labor, we recommend treating the periphery of

several large patches rather than treating only one large patch completely. This should help contain the entire infestation. Young toadflax seedlings are susceptible to mortality from competition, therefore seeding or planting native species after control treatments may reduce the number of toadflax seedlings that are able to become established. Any method of control treatment should be repeated for 5-7 years on adult plants and a total of 10-15 years to remove seedlings from the seed bank Lajeunesse et al. 1993, Lajeunesse 1999, Sheley and Petroff 1999). The long-term persistence of Dalmatian toadflax and other exotic species calls for long-term management plans that include monitoring in order for exotic species management to be successful.

Revegetation with native species is an effective way to establish plant cover, stabilize soil, and reduce exotic establishment after a disturbance. The goal of this study was to provide baseline information about 28 native species, and compare their performance to an exotic species that is often used in revegetation. We discovered that a growth chamber germination test does not accurately to predict greenhouse or field germination rates for all species. *B. dissecta* performed the best among late season forbs in the field, but performed extremely poor in the greenhouse trial. Therefore, we recommend conducting a field test for calculating expected germination or a field plus growth chamber test. Graminoids that performed particularly well in the field were *E. elymoides* (cool season grass), *P smithii* (cool season grass), and *B. gracilis* (warm season grass). Forbs that performed particularly well were *O. lambertii* (cool forb), *V. Americana* (cool forb), *L. argenteus* (cool forb), and *B. dissecta* (warm forb). Annual ryegrass did not outperform the native grasses in the field and therefore, indicates that native species are better adapted to this environment and have greater production than annual ryegrass.

In choosing a native seed mixture for revegetation a manager should select a suite of species that will be present all year in order to use available resources that would otherwise be available to exotic species. This can be achieved by choosing grasses and forbs that actively grow during the early (cool) and late (warm) part of season. Additionally, seeding cool and warm season species that provide plant cover throughout the growing season may assist in reducing invasion by exotic species, enhancing wildlife habitat and forage, and preventing

soil erosion. If grazing occurs at the site to be revegetated, a manager should also consider including species that are not palatable to ensure that plant cover remains at the site. From the species included in this study, we can recommend using the species with a high overall performance rating or with a high performance rating for specifically desired response variables.